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DISEASE IN PLANTS

DISEASE IN PLANTS

BY

H. MARSHALL WARD, Sc.D., F.R.S.

FELLOW OF SIDNEY SUSSEX COLLEGE, HONORARY FELLOW OF CHRIST'S COLLEGE AND PROFESSOR OF BOTANY IN THE UNIVERSITY OF CAMBRIDGE

PRESIDENT OF THE BRITISH MYCOLOGICAL SOCIETY, AND FELLOW OF THE LINNEAN AND ROYAL HORTICULTURAL SOCIETIES; HONORARY FELLOW OF THE MANCHESTER LITERARY AND PHILOSOPHICAL SOCIETY AND OF THE BOTANICAL SOCIETY OF EDINBURGH

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PREFACE.

It has often been represented to me that the cultivators of plants, among whom are to be included planters and foresters, as well as agriculturists and gardeners of every kind, are more particularly concerned with, and interested in, the maladies themselves of the plants they grow, than in the life-history of the fungi, insects or other organisms to which they are due, or in the physiological processes which are involved; and although it is impossible to really understand any disease unless we also understand the processes by which it is brought about, there is room for sympathy with the point of view of the cultivator. He says, in effect, "I do not want to know all about the biology of the fungus of wheat-rust, or of the *phylloxera*, nor do I want to learn what experts can tell me about the action of bacteria in soil, or the process of starch-formation in the leaves: I have neither the time nor the means to master these details. What I want is guidance as to what is wrong with my tomatoes, apple trees, chrysanthemums, fir trees, turnips, etc.,

and what I am to do to set things right." Just so. With the latter part of this cry one must sympathize, much as a doctor does with the wail of the parent who calls him in to cure his sick child—we need not stop to classify or compare the motives of the parent and the cultivator, and perhaps I had done better to select a breeder of sheep with his flock and a veterinary doctor in the illustration, but we will let it pass; and as regards the former part of the cry, I do not know that the plant-doctor can expect the cultivator to be initiated in the aetiology of the disease any more than the physician expects the parent to understand the biology of the typhoid bacillus. That both the cultivator and the parent would be the better for a real knowlege of the disease in either case must be admitted—nay insisted on, provided the knowledge *is* real—but we have to deal with facts, and it is a fact that the clients of both doctors are impatient of the details of the case.

Now, of course, I am aware that no short cut or "royal road" to science exists, and if a man is going to train up trees or other plants, he ought to know all about them in health and in sickness, in youth and in old age, and he ought to learn everything about the soil they grow in, the air that surrounds them, the enemies that beset them, and all the multifarious relations of these one to another; but when I look at my boy and reflect how much his nurse, his schoolmaster, his tutor, his doctor, and his parents *ought* to know succes-

sively and simultaneously about him in sickness and in health, and about his surroundings, etc., I begin to wonder whether there is not after all something to be said for the cultivator's point of view.

Moreover, the cultivator knows a good deal about his plants which I do not know, and although I should much like to know it, his plea of want of time rings in my ears and the conviction strikes home that one ought to try and meet his views, and tell him something about disease as manifested in plants without insisting on his becoming a professional mycologist, entomologist, agricultural chemist, and philosopher.

Of course, beyond a certain point, it is his look-out how much the information is worth, and its educational value—a very different matter—is sure to suffer from any restrictions imposed on the treatment of the subject; but if the theme of disease in plants, treated from a general point of view—I was about to write "treated in a popular manner," but that is impossible until physiology and mycology are more widely taught—enables him to understand better the questions he puts to himself, and, still more, if it stimulates him to enquire further into the inexhaustible field of science glimpsed at, something may come of it.

The purpose of these essays is to treat the subject of disease in plants with special reference to the patient itself, and to describe the symptoms it exhibits and the course of the malady, with only such references to the agents which induce

or cause disease as are necessary to an intelligent understanding of the subject, and of the kind of treatment called for. Consequently I have avoided any unnecessary classification or elaborate descriptions of parasitic fungi or insects, histological details of the tissues of plants, chemical and physical details regarding the soil, and even matters purely physiological as far as possible. Several admirable works on these subjects are already available, and must be referred to for further details.

It is, however, quite out of the question to avoid technicalities, though I have chosen the simpler course wherever it was found feasible, and have tried to so employ the examples selected that the student who wishes to go further into the matters dealt with may turn to special treatises for further information. For one eminently technical section I ought perhaps to apologise, but the temptation to try and set forth, in concrete form and suitable for the purposes of this book, some account of what is known of the most essential and profound factors concerned in the difficult question of the nature of life and death, health and disease, was great. Probably my apology should go further, and apply to what after all must be failure to explore this mystery to the bottom: my only excuse must be that it may stimulate others to go further.

It was an afterthought to add, in Part I., the considerations on the factors which influence the

plant regarded as a living machine, so to speak, in order that the student may the better apprehend the point of view taken of the bearings of the matters discussed in Part II.

With regard to references, it seemed a better plan to give, in the form of notes after each chapter, the titles of the principal books and papers on which a student may base a further course of reading, than to overweight the pages of what is, after all, merely an introductory sketch to a huge subject, with detailed quotations from the numerous sources of information made use of. I have freely expressed my own opinions, but the sources for others are, I hope, as freely given. It will, however, be understood that I have not aimed at a complete bibliography, and, particularly, I have only given foreign references where it seemed that adequate treatment of the subject could not be found in English.

My sincere thanks are due to Mr. F. Darwin, F.R.S., who has kindly looked through many of the proofs, and given me the benefit of several suggestions: and to my wife for the very material aid she has afforded me in the preparation of the index.

H. MARSHALL WARD.

CAMBRIDGE,
November, 1900.

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PART I.

SOME FACTORS.

CHAPTER I.

THE PLANT AND ITS SURROUNDINGS.

The plant the central object of study—soil, climate, atmosphere, etc., are factors of its environment. Agricultural chemistry. The plant a machine. Physiology.

If I were asked to sum up the most important result of the numerous advances made during the past decade in agriculture and forestry, I should reply—the clearer and wider recognition of the fact that the plant itself is the centre of the subject, and not the soil, climate, season, or other factors of its environment. Until comparatively recent times it was the habit of farmers, foresters, planters, and gardeners, all the world over, to look upon the plant as a mere item or as a mysterious if important one in their calculations, and to regard the soil as the chief factor in their studies.

Now all is changing, and the world is gradually awakening more and more to the recognition of the truth that the soil and the clouds and the

atmosphere are merely reservoirs of more or less inert materials, from which the living plant draws its supplies, and works them up, by means of energy focussed from the sun, into new plant substance.

In other words, the more far-seeing pioneers of scientific agriculture and forestry, etc., are recognising that agricultural chemistry is not the be-all and end-all of agricultural science; but that, in place of the study of the chemical analyses of dead soil, water, air, and plant-remains, which has so long held sway, largely owing, I think, to the influence of Liebig, the student should have his attention more concentrated on the living plant itself and on the physiological actions which make up its life. He must regard the living plant as a sort of working machine—infinitely more complex than any machine made by man, but a machine nevertheless—the purpose of which is to store up energy from the sun, and so to add to our wealth on this planet, at the expense of the extra-terrestrial universe.

It is not, be it noted, that the new study proposes to ignore or abandon the old studies: modern physiology owes too much to the physics and chemistry on which it is partly based, and to the labours of De Saussure, Ingenhousz, Priestley, and others, for that. But it is that the new study recognises that the central point, to which all views must be focussed, is not the one that it was formerly supposed to be. The student is still taught that the chemistry of soils yields

valuable information, and that lessons of importance are derived from comparisons of the analyses of the ashes, etc., of plants; but he is no longer able to cherish the hope, however remotely, that such studies solve his most important problems.

The scene—or rather the point to which attention is now directed—is the living, working, energy-accumulating plant itself, and not the dead store of materials in the soil. The reason for the change is not far to seek: it is due to the enormous strides made in the study of the physiology of plants during the last quarter of a century, and the subject abounds in examples illustrating the marvellous advances that have been made, and at the same time showing how, in the progress of researches, made for their own sake—*i.e.* in pursuit of satisfaction for the intense curiosity of the scientific man—all kinds of side issues turn up which prove to be of value in practice, and suggestive of further thinking.

At the beginning of the nineteenth century—*i.e.* about 1820—the best thinkers were giving up the old ideas that the environment supplied food, as such, to plants, and had recognised that the plant takes up substances from without and rearranges these in its own body.

The next twenty years or so form a very dark interval in plant physiology, chiefly owing to the influence of the assumption of a special "vital force," an assumption which was not allowed merely to serve as a hypothesis put forward to stimulate

research and suggest better ideas, but which gained a hold over men's powers of reasoning to an extent which now appears monstrous and phenomenal.

Many errors crept in during this reign of terror, one of the most fatal of which was De Candolle's revival of the idea of "spongioles"; and another, equally disastrous in many of its effects, was the conception of a sort of vegetable food-extract, humus, existing in the soil in a form peculiarly suitable for direct use by plants. It was during this period that the confusion between the processes of respiration and carbon-dioxide assimilation arose, and exerted its effects for evil into our own day.

The now astounding statement that oxygen-respiration in plants did not occur, laid the foundation of many subsequent difficulties, and so did the positive and authoritative views on the uses of minerals to the plant. Liebig, in fact, stood in the invidious position of being a high authority on purely chemical questions, who was impelled to give opinions on matters which can only be solved by physiological experiments: his great service was to clear up mistakes as regards the chemistry of soils and of plants—his great mistakes were due to his pronouncing on physiological matters; and it may be doubted whether his great services to the purely chemical side of subjects connected with agricultural matters are the more to be admired, or the disastrous influence of his statements on subjects which do not belong to the

domain of chemistry should be the more deplored. Be that as it may, he handed on to succeeding generations some weighty errors as regards plant-life, and taught the agriculturist to regard chemical analyses of soils and plant ashes with a reverence which obstructed progress for some time. As a set-off to this we must place his contributions to the destruction of the bugbear vitalism, which was simply preventing enquiry, and his services in bringing together and sifting with power and originality all that had been then acquired as regards the chemistry of the plant, the soil, and the atmosphere.

That Liebig was indispensable in 1840-1850 is one thing; but that his influence should extend to the present day is quite another, and his inevitable mistakes were almost as powerful for future evil, as his clear exposition of the chemistry of his day was productive of immediate good.

Boussingault, working at the same time, 1837-1855, but experimentally with the living plant, taught us more about these matters than any investigator of the time, though it is very probable that the stimulus of Liebig's speculations, good and bad, had its effect in impelling Boussingault to devote his splendid methods to problems of plant-nutrition. Boussingault's contributions to our knowledge of the composition of the dead plant cannot be over-estimated; but he did more than this, because he so clearly apprehended the necessity for asking his questions directly of the living plant, instead of deducing

from chemical principles what might be supposed to occur in it; and although future researches showed that even so careful an investigator solved a problem of first importance—viz. the question of the fixation of free nitrogen—the wrong way, it will be found that so far as he did go his conclusions were sound, and well calculated to inspire the confidence with which the world received them. As we are here concerned more especially with the botany of agriculture, however, it is unnecessary to dwell longer on these matters, or on the similar and even more extensive experiments, of world-wide reputation, carried on for so many years, and still being carried on under the liberal auspices of Sir John Lawes, at Rothamsted. Moreover it may be necessary to return to some of these points later on.

Notes to Chapter I.

The reader will find a further general account of these matters in Sachs' *Lectures on the Physiology of Plants*, especially Lectures I. and XII., Engl. ed., Oxford, 1887. He may then proceed to Pfeffer's *Physiology of Plants*, Engl. ed., 1899, chapter I., and to the account of the history of the subject in Sachs' *History of Botany*, Oxford, 1890, especially pp. 359-375 and 445-524. References to more special literature will be found in Pfeffer.

CHAPTER II.

THE PLANT AND ITS FOOD.

The food of plants—"Vital force"—Other errors—Liebig and Boussingault—The botany of agriculture. The synthesis of carbohydrates—The physiology of plant-nutrition. The persistence of misconceptions.

THE year 1860 may be regarded as a landmark of importance in the history of plant physiology, for it was in that year that Sachs discovered that the bringing together of water and carbon-dioxide, in the green chlorophyll-corpuscles of the plant exposed to sunlight, results in the formation of the grains of starch found in these corpuscles.

Previous to this date Dutrochet (1826-37) had introduced the then crude idea of osmosis into physiology; vegetable anatomy had improved, and the modern conceptions of the living cell, protoplasm, nucleus, etc., were slowly looming; sieve-tubes had been discovered, and the proteids and starch in various parts of the plant examined; and the suggestion was abroad, replacing Liebig's

idea that plant acids were the first products of carbon-assimilation, that some substance, of a slimy nature, was manufactured in the cells of the leaves and thence distributed as the formative material from which the plant constructed its parts. Davy and Boussingault had even surmised that a carbohydrate might be the first-formed product in assimilation.

There can be little doubt that Sachs' classical proof, by direct physiological observation and experiment, first brought forward the truth of organic synthesis in the plant in a concrete and convincing form.

But it did more than that. It laid the foundation of the modern physiology of plant-nutrition on ground already prepared by De Saussure and the earlier workers; for, in addition to emphasising the truth of organic synthesis—a truth which had been gradually impressing itself on the world for some years—Sachs' discovery showed clearly the real meaning of carbon-assimilation as a process for obtaining combustible food, which the plant then proceeds to make use of.

Many points were rapidly cleared up at once, or if not explained were at least put into a strong light for further enquiry, and plant-nutrition soon ceased to be the mysterious subject for all kinds of wild conjectures that it had hitherto been.

The meaning of thin leaves, with numerous stomata and finely ramified or divided vascular bundles, became more apparent, as also did the significance of the ascending transpiration current;

the storage of starch-grains in tubers, medullary rays, roots, seeds, etc., obtained meanings not understood before; the spread of roots in the soil, and the gradually discovered properties of the finer rootlets and of the root-hairs, fitted naturally into their places; and, in short, a thousand facts, otherwise isolated, became collated into an intelligible system, full of suggestions for new work, such as has since gone on and is now being pursued with an activity and success never before realised in the history of science.

As time went on, while the general truth of Sachs' views was confirmed, a number of detailed discoveries were made which seemed to contradict them in certain points. It was found that not all leaves form starch, for some contain sugar or oil; but Holle and Godlewski proved experimentally that this oil may be replaced by starch if the conditions of assimilation are slightly modified. More recently Hébert discovered that the stalks and leaves of grasses contain a peculiar form of gum, which was formerly confounded with starch, a substance not abundant in them. Then came Schimper's discovery of starch-forming corpuscles, which, if supplied with sugar, are able to form starch-grains in the dark, as in tubers, etc., underground; and as subsequent researches have proved that the chlorophyll-corpuscles—which are morphologically the same as the starch-forming corpuscles and can be replaced by them—are also able to form starch-grains from sugar, as proved by the experiments of Boehm, Acton, Meyer, Laurent,

Bokorny, Saposchnikoff, and others, it soon became evident that nothing essential needed altering in Sachs' view that starch is the first visible product of carbon-dioxide assimilation, only it became clearer that the starch-grains are built up by the protoplasm from glucose or some similar body, and represent so many packets of reserve materials put by for the present because not required for the immediate needs of the cell.

Boussingault showed, about thirty years ago, that assimilation soon stops in green leaves if cut off from the plant, not because the leaves die, but owing to some "maximum capacity" being attained. Sachs had shown that the starch passes down to other parts of the plant in solution as glucose.

Neither time nor space will permit me to go into the enormous field of research and results opened up by these and similar observations made between 1860-70. It must suffice to say that they led to the discovery and study of the diastatic and other enzymes in the leaves and other green parts of plants, and to a clearer understanding of what was already known of them in seeds, and this knowledge reacted at once on our insight into the processes of transport of reserve materials and constructive materials from one part of the plant to another, matters which will be referred to later on.

It remains to explain Boussingault's difficulty as regards the cessation of assimilation. Recent researches confirm the view that at least three

causes are at work to bring about the inhibition of the carbon-assimilation: first, the chlorophyll-corpuscles become filled to excess with starch, which cannot get away because all the passages are full and the products are inhibiting the further action of the enzymes which should dissolve the solid granules; secondly, the leaf being detached from the plant explains why the soluble products cannot get away, for this makes a great difference in the rate of exhaustion of the leaf; and, thirdly, the same fact involves that the leaf can obtain no further supply of salts of potassium, etc., without which elements the processes in question cannot go on.

These and numerous other deeper insights into the process of assimilation, obviously strengthen the force of Sachs' discovery; though it by no means necessarily follows that starch-grains are always the resting form of the products of assimilation, and we now know that such is often not the case: we now have much deeper glimpses into the initial products of carbon-assimilation than Sachs had in 1860, but this enhances rather than detracts from the importance of his splendidly worked-out discovery. Put more generally, we may now say that the process of carbon-dioxide assimilation in green leaves under the influence of light is a process of synthesis—photo-synthesis—resulting in the building up of a carbohydrate such as sugar, inulin or starch from the elements carbon, hydrogen and oxygen.

But it must not be supposed that the importance of Sachs' discovery, and the rapid consequent

extensions of our knowledge, did their work forthwith in disabusing men's minds of old and erroneous notions. To say nothing of numerous smaller misconceptions which still held their ground owing to the stupendous ignorance of plant-physiology which prevailed, we find incompetent teachers and text-books were still propagating ideas worthy of ancient times. The confusion between oxygen-respiration and the gas interchanges in carbon-assimilation was by no means eliminated even recently, though it can no longer withstand the deliberate onslaughts now made on it. That the roots take up food as such from the soil, and that that food is directly employed by the plant for its nutrition is even yet implied in daily conversation around us; and although matters have advanced so far that everyone now knows that the substances at the roots must be in solution, ere they can be received into the plant, it sometimes leads to astonishing replies, if we press the question very far as to how the absorption takes place, in an elementary examination of agricultural students. That manures are foods to the plant, that sap circulates, that transpiration is of use to keep the plant cool, and wood is a "porous body," etc., are only a few of the misconceptions still current, in a decade that has found publishers for a work advocating that roots are congealed sap, and that the leaves of plants absorb the moisture and dust of the air, and so provide the plant with food, and for a paper explaining

the action of root-hairs as tubes with open pores at their tips. But the gravest misapprehensions current among us are due to the crude ideas as to what a plant really is: this, I take it, is owing to the difficulty of grasping what physiologists mean by organised structure, and leads to regarding the living being either as a mere aggregation of chemical compounds, built up by the ordinary play of chemical forces, as we know them, acting on dead matter, or, as in the days before organic chemistry, as a mysterious entity endowed with "vital force," and with properties not amenable to scientific investigation. The mistaken notions as to the powers of roots to "select" those substances which the plant requires, and to reject useless ones was merely an expression of this belief.

The rock on which all are liable to come to grief—the chemist or physicist who requires all his facts in terms of analyses and proportions by weight, and therefore takes too mechanical a view of the subject, or the man who is not scientifically trained at all, and therefore is more liable to go to the other extreme and regard the plant as a mysterious something which grows and has poetical associations and traditions—is the great fact of organised structure, and it is the recognition of this fact and some of its consequences which has altered the whole position of the subject, and brought the study of the plant into the domain of physiology. The living plant, its structure and organisation, the functions of its

mechanism, and its relations to the environment, thus forms a subject apart from that which concerns the chemical composition of the plant and its environment, and this distinction designates, in a word, as it were, the change which has been brought about by modern biology.

A point to be emphasised to the utmost where agricultural students are concerned is that the essential process of feeding is the same in a green plant, a fungus, and an animal; the greatest confusion still exists with regard to this matter, owing to misconceptions as to the real meaning of the functions of the chlorophyll-corpuscles when supplied with carbon-dioxide and water and the energy of the sun's rays. The plant does not feed on carbon-dioxide, any more than it feeds on oxygen—it feeds on the organic material after it has been constructed, and the chlorophyll-function is merely one mode of obtaining supplies of such organic substance.

Notes to Chapter II.

In addition to the references in the last chapter, the student should consult Sachs' *Lectures*, XVII.-XIX., and Pfeffer's *Physiology*, pp. 287-329, for the further development of this subject. An excellent résumé, with new facts and points of view, will be found in Dr. Horace Brown's "Address to the Chemical Section," *British Association Reports*, Dover, 1899; and "Chemistry and Physiology of Foliage Leaves" in *Trans. Chem. Soc.*, 1893, p. 604. See also Blackman, "Experimental Researches on Vegetable Assimilation and Respiration," *Phil. Trans.*, 1895; and Parkin, "Formation, etc., of Carbohydrates in Monocotyledons," *Phil. Trans.*, 1899.

CHAPTER III.

THE PLANT A LIVING MACHINE.

The plant a machine into which energy and material are taken—Carbon assimilation—Feeding—Accumulation and transformations in the plant. The action of light—The chlorophyll-function.

THE relations of the plant to the environment can only be understood by taking into account the results of modern physiological discoveries. These teach us that the living plant is a highly complex machine, the details of its organisation and structure being much more numerous and much more closely correlated at numerous points, than the parts of any other machine known to us.

They also teach us that it is supplied with energy from without, as any other machine; and that when so supplied, and properly working, the living structure or machinery does work, also as other machines. But modern physiology goes further, in that it renders some account of the ways by which the external energy is taken into

the plant, and there applied to do work, or stored up for a time in order that it may be used to do work at some future time.

The accumulation of energy thus ensured is associated with corresponding changes of material substance, and the principal means for bringing this about is recognised in the assimilation of carbon-dioxide—photo-synthesis.

In this process energy enters the chlorophyll-corpuscle in the form of the radiant energy of the sun, it is there directed in the mechanism of the protoplasm, so as to do work on the molecules of water and carbon-dioxide which have also been brought into the machinery; this it does, breaking asunder their stable structure into unstable bodies, which then re-combine in different ways to form a carbohydrate, such as starch, and this starch is temporarily stored as grains, while oxygen escapes.

Each starch-grain, therefore, is to be regarded as a packet of matter and of potential energy, as it were, capable of yielding up the latter at any future time, when put under such circumstances that it must do so. Such stores of energy-yielding substance, if I may use the much-abused phrase, form the principal food of the plant—or of an animal, if it steps in and takes them—and we now see that the process of carbon-dioxide assimilation, as it has perhaps unfortunately been called, is not the same thing as the process of feeding, for the *feeding—i.e.* the nutrition proper—of the plant does not begin until the *food* has been thus obtained.

We now see what the real position of the plant is, to its environment, whether the latter be living or dead. From our point of view, the plant serves as a centre for bringing together the substances obtainable from the soil, and those derived from the atmosphere, and so focussing and directing the radiant energy of the sun upon these substances, that they are broken up, and some of their constituents synthesised, with absorption of energy, into a body, such as starch, containing more energy than did the original substances taken together or separate. It matters little whether the actual carbohydrate thus synthesised is starch, or sugar or inulin: the point is that energy has been gained from outside and bound up with the acquired material for further use. But modern physiology has carried matters much further than this, and especially in the three following directions.

In the first place, it has shown that much of the energy thus stored from without in the plant is again liberated in the process of oxygen respiration, and expended partly as appreciable heat and partly as driving force for stimulating the machinery of the living plant to further activities.

In the second place, part of it is rearranged with the rearrangement of the molecules with which the energy is bound up, as it were, so that work of various kinds is done *in* the machinery of the plant: I refer to various metabolic and surface-actions resulting from the peculiar mode of presentment of the resulting substances, for

instance the production of osmotic pressures in the cell.

And, thirdly, part of the synthesised substance is worked up into higher bodies, by processes which obviously entail the further doing of work on the constituents.

The further pursuit of this theme would evidently carry us beyond the more immediate subject of this book; but I want to make clear that recent researches render it more and more certain that the living plant is a complex piece of co-ordinated machinery which brings together matter and energy from the external universe, and then gets work out of these.

This proposition is the more important because the whole question of the enrichment of our planet with new food, new building materials, and new fuel, to compensate the daily losses, depends on it, and is of course to be referred fundamentally to the acquirement of new supplies of energy from the sun. Enormous activity has been displayed by physiologists, since 1860, in attempting to solve the question, which of the many different rays known to proceed from the sun are absorbed by the chlorophyll-corpuscle, and directed to the performance of the work above referred to.

The names of Draper, Sachs and Pfeffer stand forth prominently as pioneers in this; while those of Lommel, Engelmann, Timiriazeff and Langley have been among the most active in making important contributions to the subject, and in attempting to answer the further questions con-

nected with the mode in which the chlorophyll is concerned in utilising the energy of the solar radiations. The point is one of supreme importance, because it goes on all fours with modern questions as to the rays of light absorbed or dispersed in our atmosphere at different seasons of the year, or in special climatic conditions, to say nothing of its other scientific aspects. Unfortunately, however, we have no satisfactory explanation of the actual rôle played by the chlorophyll substance itself, in spite of much industrious work which has been done in the subject in this country and elsewhere. As regards the rays employed, it was first proved that the most effective belong to the red end of the visible spectrum, and that the effect as measured by the amounts of oxygen given off, and of starch formed in given periods of time, is more or less proportionable to the intensity of the solar light. Then it was established that no monochromatic light is so powerful as the white light from which it was obtained, though the relative numbers expressing the activity in the red and yellow regions may stand to those in the blue as something like 12 : 1. The latest results place the maximum assimilation in the red-orange, and this coincides with the maximum absorption in the chlorophyll. If we may accept the current views as to the distribution of energy in the spectrum of solar light, which depends on the complete absorption of all the rays by a black body, where they are estimated as heat, we have

the interesting result that the agricultural or forest plant is adapted to catch and retain, broadly speaking, just those particular rays which possess most energy.

The probability is increasing that the protoplasmic machinery is the really effective mechanism in the process, and we may figure this machinery as so holding or presenting the molecules of carbon-dioxide and water to the impact of the light-vibrations, that the latter are enabled to undo the molecular structure; the atomic combinations thereby liberated may then be supposed to form a body like formic-aldehyde, which by polymerisation becomes a carbohydrate of the nature of a sugar such as glucose, which the protoplasm then builds up into its substance and subsequently deposits as starch, and stores temporarily in the form of grains or as amorphous material.

This is partly hypothetical, and is largely due to the careful deductions of the chemists, but there are very many facts now to hand which bear out its probability, especially the recent advances in our knowledge of the sugars, and the experimental feeding of leaves and plants deprived of starch with such substances as dextrose, levulose, maltose, and other sugars, as well as glycerine and other bodies which should be convertible into, or yield them, if the theory is true. In this last connection, the careful and extensive experiments of Acton, A. Meyer, Boehm, and Laurent should be mentioned. It would be interesting to enlarge upon Engelmann's beautiful physiological experi-

ments in connection with this subject of absorption of solar energy, where the maximum accumulation of oxygen-loving bacteria at those parts of a green alga which lie in the red-orange of the spectrum, are used as indicators of the maximum oxygen evolution (and therefore of the maximum carbon-dioxide assimilation), but space will not admit of this. For a similar reason I must also pass over the same observer's experiments with plants which assimilate in protoplasm behind a red instead of a green substance, and which absorb chiefly other rays between the yellow and blue, with the remark that they also seem to imply that it is the protoplasmic machinery which turns the energy on to the carbon-dioxide molecule, the coloured screen being secondary in the matter. Recent experiments which show that green plants will not assimilate carbon-dioxide in a light which has passed through a solution of chlorophyll—and therefore left its red rays behind; nor behind a screen of iodine dissolved in carbon-dioxide—which lets no visible rays between the red and blue pass—should be noticed, as showing the importance of the chlorophyll and the special rays referred to, however; and I ought at least to mention Timiriazeff's beautiful proof, published in 1890, that if, on the leaf of a plant left in the dark long enough to render it free of starch, a bright solar spectrum is steadily projected for 3-6 hours, the chlorophyll then removed by alcohol and the decolorised leaf placed in iodine, the image of the spectrum is reproduced by the different intensities of the starch bands, blue with

iodine, in the different parts. Here, again, the maximum coloration coincides with the maximum absorption in and near the red.

Microscopic observations and photo-chemical experiments alike convince us that the chlorophyll-corpuscle is itself a complex piece of protoplasmic machinery, working for and with the rest of the plant, and there can be little question as to the greater accuracy of our reasoning on the whole question I am discussing, since Meyer, Schimper, Pringsheim, and others have established the importance of its structural peculiarities.

I must now pass on to consider another aspect of the question of carbon-assimilation.

Notes to Chapter III.

In addition to the references in the last chapter, the reader may be referred to Sachs' *Lectures*, XXV., and Pfeffer's *Physiology*, pp. 329-356, where the voluminous literature is given.

CHAPTER IV.

METABOLISM.

Quantities of starch formed, and their significance for the plant. The absorption of energy—the conversion of energy in the plant. The plant is a complex machine for concentrating and storing energy and material from without.

SACHS measured the increase in dry weight (due to the carbohydrates formed in the chlorophyll-corpuscles) per square meter of leaf-surface, exposed for a definite period, by drying rapidly at 100° C. equal areas of the leaves concerned, and comparing the weights.

Of course the results are not to be pushed too far, in view of the fact that some of the starch is continually passing away to be utilised, and of the difficulties of comparing the weather, the intensity of light, currents of air, hygroscopic conditions of atmosphere, and other variable factors which influence the matter. For instance, the stomata open and close to different extents according to

the conditions of light and moisture, and this affects the whole mechanism of transpiration especially, and therefore the supplies of water and mineral salts. Nevertheless, some interesting and valuable results have been obtained in connection with this important subject.

It was found, for instance, that the foliage of a sun-flower or of a vegetable-marrow may be forming starch at a rate of considerably over a gram per hour in every square meter of leaf-surface exposed on a fine day; while in particularly clear and warm sunny weather Sachs obtained as much as 24 to 25 grams per square meter per diem.

When one reflects that 200 square meters is not an extravagant estimate for the area of leaf-surface exposed on a tree, for a period which even in our latitudes may be considerably over 100 days of, say, ten hours' light, we need no longer wonder at the rapidity with which wood is produced in the stems, and similar estimates (which I have purposely kept lower than the estimates for continental and tropical climates) may suffice to show how quickly potatoes or the ears of corn, etc., may fill up with the starch or other carbohydrates which render them valuable as crops. We want more measurements in these connections, moreover, for there are several ways in which they are of scientific value and practical importance.

It is evident from what has been said that every grain of starch formed represents so much

energy, packed away for the moment in the storehouses of the plant; and we know that—quite apart, however, from intermediate transformations of the energy thus stored—this energy reappears in the kinetic state eventually, when the starch is burned off, in presence of oxygen, and transformed into carbon-dioxide and water. It matters not how quickly or how gradually this combustion occurs, or whether it is accomplished by burning in a fire, or by slow and complex stages in respiration or metabolism: the point is that the unit of weight of starch yields so many units of heat when its structure tumbles down to the original components, carbon-dioxide and water.

Clearly, if we know how many units of heat are yielded by the combustion of one gram of starch, we can obtain an estimate of the amount of energy, measured in terms of heat, which the foliage gains and stores up—an estimate which will approach the truth in proportion as our estimate of the total assimilative activity is correct.

A word of warning is necessary here, however, for those best acquainted with physiology recognise that however useful such calculations as the above may be, and undoubtedly are, to give a general idea of the fact that the energy represented is large, it would be a mistake to suppose that such estimates give even an approximate measure of the energy of potential which may be got from the carbohydrate, and still less of the amount of work that may be got from its employment, according to the way it is employed or presented

in the plant. To take a single instance only. If the carbohydrate is rapidly burned off to carbon-dioxide and water, very little is got out of it in the way of work—most, if not all, of the energy set free escapes as heat: whereas if the carbohydrate is slowly and gradually oxydised, passing through various stages and giving rise to powerfully osmotic bodies in the process, or if it is built up into protoplasm, or into the structure of a cell-wall, relatively enormous quantities of work may be got out of its surface-energy, and heat may be absorbed. Whence it follows that we cannot measure the power for physiological work of a body by merely obtaining its heat of combustion, any more than we can infer its significance in metabolism from its chemical properties.

The general conclusion that the plant stores large quantities of energy may of course be arrived at by simply estimating the enormous quantities of food-material which we obtain annually from agricultural plants.

Modern physiologists have attempted to proceed further than this, however, in their essays to form an estimate of the relations between the available energy in the solar rays and that used and stored in the plant.

If we reflect on such phenomena as the cool shade of a tree, and the deep gloom of a forest, and on experiments which show that an ordinary leaf certainly lets very little of the radiant energy of the spectrum pass through it, it becomes evident that many of the rays which

fall on the leaf are absorbed in some form, and it becomes very probable that much of the solar energy, other than that we term light, is retained in the leaf for other purposes than assimilation—or, at least, no other conclusion seems possible in view of all the facts. Engelmann's researches with purple bacteria are almost conclusive on this point, and we may regard it as extremely probable that the plant makes other uses of rays, perceived by us as heat-rays, as sources of energy. Researches on the influences of temperature on assimilation and other functions point to the same conclusion; and Pfeffer and Rodemann definitely state that heat is converted into work in the osmotic cells. And the study of the absorption bands in the spectrum of the living leaf becomes more intelligible in the light of these conclusions. Moreover, the fact that a plant still carries on processes of metabolism when active transpiration has lowered its temperature below that of the surrounding air—and the plant therefore receives heat from the environment—points to similar conclusions.

The importance of the conclusion is immense, for even if the plant had no other sources of energy than the darker heat rays of the solar spectrum, it is clear that it ought to be able to do work.

The above may suffice for the general establishment of the conclusion that the plant absorbs more radiant energy than it employs solely for assimilation, and emphasises our deduction that it is a machine for storing energy.

The question now arises, how is this relatively enormous gain in energy employed by the plant? Our answer to the question is not complete, but modern discoveries in various directions have supplied clues here and there which enable us to sketch in some degree the kinds of changes that must go on.

Not the least startling result is that, important as carbon-assimilation is as the chief mode of supplying energy, it is not the only means that the plant has of obtaining such from the environment, and it is even possible—not to say probable—that energy from the external universe may be conveyed into the body of the plant in forms quite different from those perceptible to our eyes as light.

In the most recent survey of this domain, it is pointed out that we may distinguish between radiant energy, as not necessarily or obviously connected with ponderable matter, and mechanical energy, which is always connected in some way with material substance. All mechanical performances in the plants depend on transformation of some form of these, evident either as actual energy doing mechanical work, or as energy of potential ready to do work.

In so far as molecular movements are concerned, we have the special form of chemical energy. The evolution of heat, light and electricity by plants are instances of radiant energy, and so on.

Many transformations of energy in the plants are due to non-vital processes—*e.g.* transpiration,

warping actions, etc., but we cannot always draw sharp lines between the various cases. Nor can we directly measure the work done in the living machinery; but from the effects of pressures and strains, the lifting of heavy weights, driving of root-tips into soil, osmotic phenomena, etc., it is certain that the values may be very high.

The following classes of processes in living protoplasm and cells may be taken as indicators. First we have transformation of chemical energy, without which continued life is impossible: in many cases—*e.g.* the processes connected with oxygen respiration—these result in the development of heat. Secondly, we have those remarkable manifestations of energy known as osmotic processes, which depend on surface actions, and with which may be associated other surface effects, such as imbibition, secretion, etc., and in connection with which heat may be evolved or absorbed. It is true the substances which exhibit the properties here referred to may be produced, or placed in position, by chemical energy, or they may be absorbed by roots, etc.; but the proximate energy exhibited by them is not derived from chemical energy, and may be out of all proportion to the chemical energy of the substance or substances concerned. Moreover it is significant to note that a highly oxydised body may develop much osmotic energy, as well as a highly combustible one.

It is of the greatest importance to realise the truth that much work can be, and is done in

the living plant, by conversions of energy of potential independent of and out of proportion to the chemical energy available by decomposing the substances concerned; even the heat of respiration may be superfluous here, for the plant may absorb heat from without, and convert it into work.

Tensions often arise in the plant, and do work expressed as movements—*e.g.* the springing of elastic Balsam fruits, stamens of *Parietaria*, etc.

Osmotic energy not only results in enormous pressures and tensions, but causes movements by diffusion and diosmosis, and any given osmotic substance which carries this energy with it is not necessarily formed always in the same way in the cell—*e.g.* glucose may arise from starch, or from carbon-dioxide, or from oil.

Surface-energy is also expressed in the powerful attractions for water exhibited in imbibition, swelling, capillarity, absorption, surface tensions, etc.

Transpiration induces relatively enormous disturbances of equilibrium, and does work in moving water quite independent of chemical energy.

Again, what may be termed excretion-energy, as expressed in the separation of a solid body—*e.g.* a crystal—from a solution, may be for our purposes regarded separately. Any change in the condition of aggregation of a substance in the plant may result in movements and the overcoming of resistances.

It will be evident from this short digression—and this is the point I wish to emphasise—that in

the interval between the securing of a grain of starch, representing so much energy won from the external universe, and the reconversion of this grain into its equivalent carbon-dioxide and water, by respiration, resulting in the loss of the above energy as heat, the starch referred to may have undergone numerous transformations in the living machinery of the plant, and have played at various times a rôle in connection with the most various evolutions of energy.

If we try to picture a possible case, we may take the following. A given starch-granule, after being built up in the chlorophyll-corpuscle, is decomposed, and yields part of itself as glucose, which passes down into other parts of the plant in solution. Part of it is merely re-converted into starch, and temporarily stored: another part passes into the arena of oxydation-processes, the sum of which constitute respiration, and may serve for a time in the molecules of an organic acid: yet another part may be converted into a constituent of the cellulose cell-walls; while part may be brought into play in the reconstruction of protoplasm.

In this last connection a discovery made by Schulze about 1878, and followed up later by Pfeffer, Palladin, and others is of importance. Seedlings growing in the dark, or in an atmosphere devoid of carbon-dioxide in the light, become surcharged with nitrogenous bodies known as amides, formed during the breaking down of the proteids in the destructive process preceding and

accompanying respiration: if the seedlings are allowed free access to light and carbon-dioxide, however, the amides disappear. The explanation is that they are combined with some of the materials of the carbohydrates, and again built up into the material of the living protoplasm.

Returning to our hypothetical starch-grain—or, rather, its parts—we have some of it retained as starch, in excess, simply because it is not needed at the moment: another portion gives up its energy in respiration, and this does work on the spot, or is lost as heat; or in the body of an organic acid, or its salt, the part in question may do lifting or pressing work by osmosis, or cause diffusion-currents from one cell to another. In the constitution of the cell-wall we may have part of our starch-grain aiding in imbibition or in the establishment of elastic tensions in turgidity: and, finally, parts may be built up into the living protoplasmic machinery of the plant.

What is true for the starch-grain is also true for any particle of salt, or water, or gas which enters into the metabolism of the living plant, regard being paid to the particular case, and circumstances in each case.

Enough has been said to show that the plant cannot be properly studied merely as the subject of chemical analysis or of physical investigation; you might as well expect to understand a watch by assays of the gold, silver, steel and diamonds of which its parts are made up, or to learn what can be got out of the proper working of a lace

machine by analysing the silk put into it, and the fabric which comes out, and by taking the specific gravity of its parts and testing the physical properties of its wheels and levers.

This is not the same thing as denying the value of such knowledge, in the case of either the dead machine or the living plant: it is merely emphasising the supreme importance of the study of the structure and working of the active machinery in both cases.

Nor is it pertinent to remark on the apparent hopelessness of physiology being at present able to explain the seemingly infinite complexity of the living machinery of protoplasm and its activities. The modern locomotive is also a complex affair in its way, but it is profitable to investigate it and to know all one can of its working and possibilities, for obvious reasons: a little reflection will convince us that it is also worth while to investigate that complex machine, the plant—the working organism which alone can really enrich a country. Moreover, we ought to be encouraged by the satisfactory progress now being made, and the splendid practical results which are accruing, rather than dismayed by the prospect of unflagging labour which will be required in the future.

Enough has perhaps been said to establish the general truth that the plant is a complex machine for storing energy and material from outside, and we have seen that modern research has at least gone a long way towards determining how the living machine works.

It is hardly necessary to point out that important practical consequences may result from these phenomena of the accumulation of surplus starch or other carbohydrates in the leaves during the day, and of their disappearance during the night into the lower parts of the plant. For instance, foliage cut for fodder in the morning is far poorer in starch than if cut in the evening, and it would be very instructive to have experiments made on a large scale to test the result of feeding caterpillars or rabbits, for instance, with mulberry, vine, or other leaves in the two conditions.

Again, we now see what complications may arise if a parasitic organism gains access to the stores of carbohydrates in process of accumulation, or attacks and injures the machinery which is building up such materials, etc.

Notes to Chapter IV.

The student who desires to pursue this subject further should read Sachs' *Lectures*, XX. and XXV., and Pfeffer's *Physiology*, pp. 442-566, but he will hardly arrive at the best that has been done without consulting Pfeffer's "Studien zur Energetik der Pflanzen" in the *Abhandl. der Math.-Phys. Classe der Kgl. Sachss. Gesellsch. der Wiss.* (Leipzig, 1892), p. 151; and Kassowitz, *Allgemeine Biologie* (Vienna, 1899), Bk. I., pp. 1-127.

CHAPTER V.

ROOTS AND ROOT-HAIRS.

Older views as to root-hairs—Root-hairs and their development — Surface — Variations — Conditions for maximum formation — Minute structure — Adhesion to particles of soil—Functions.

On the roots of most plants are to be found delicate, silky-looking, tubular prolongations of some of the superficial cells, known as root-hairs. Malpighi (1687) seems to have been the first to observe them, and he took them for capillary tubes. Grew (1682) seems to have been responsible for the view that the roots act like sponges in taking up water.

Simon (1768) was probably the originator of the idea that these root-hairs were excretory tubules, a view that became very popular at the beginning of this century.

Meyer (1838) was perhaps the first to give a comparative account of them, and he supposed

them to be delicate prolongations of the root-surface to facilitate the absorption of water.

The real importance of these organs, however, has only become apparent since Sachs, in 1859, recognised their relations to the particles of soil between which they extend and to which they cling.

In 1883 Schwarz made a very thorough study of their biological character, and in 1887 Molisch gave us new facts as to their physiology. Our knowledge of them has been rendered very much more intimate by the researches of Pfeffer and De Vries on osmotic and plasmolytic phenomena, and they serve as an excellent study of some of the best results of modern physiology.

In the normal case, such as is exemplified by a seedling wheat or bean, the root-hairs arise some distance behind the growing tip of the root, an obvious adaptation which prevents their being rubbed off by the soil, as they would be if developed on parts still actively lengthening. As those behind die off, new ones replace them in front, and so we find a wave of succession of functionally active root-hairs some little distance behind the tip of the root: the same order of events holds for each new rootlet as it emerges from the parent root, and so successive borings in the soil, made by the diverging root-tips, are thoroughly explored by these root-hairs.

Measurements have shown that in various plants the surface of root on 1 mm. of length is

increased by the root-hairs in proportions given in the following table:

Plant.	Area of surface without root-hairs.	Area of root and hairs.	No. of times greater.
Maize, - -	4.52 sq. mm.	25.13 sq. mm.	5.5
Pea, - -	4.71 „	58.33 „	12.4
Scindapsus, -	14.02 „	261.9 „	18.7

- -which sufficiently establishes the general proposition that the area of the root-surface is enormously increased by these hairs.

But this does not give us any definite idea of the length of the cylinders of soil explored by these surfaces, until we find that plants such as an ordinary sunflower, hemp, or vegetable-marrow may have roots penetrating into a cubic meter of soil, in all directions, and so closely that probably no volume so large as a cubic centimeter is left unexplored. Clark found by actual measurement that the roots of a large gourd, if put end to end, extended over 25 kilometers, and Nobbe gives 520 meters for the roots of a wheat. Vetches may go nine feet deep, and oats more than three feet. The Sal, a tree of the forests of India, has roots which penetrate to a depth of 50 to 60 feet.

Some rough notion of the lengths, superficies and penetrating capacities of the roots of a large tree may be gathered from the above, but it is doubtful whether we can form any adequate ideas as to the millions of root-hairs which must be

developed along the course of these subterranean boring organs.

One of the most striking results of modern enquiry into these matters, is the discovery that the number and superficial area of these root-hairs, on one and the same plant, may vary to a large extent according to the structure, as it were, of the soil, and the degree of moisture it is capable of retaining; or, with the same soil, according to the amount of water which it receives and holds. Correlations have also been observed between the development in length and surface of the rootlets themselves.

The following illustrations will suffice to show this:

Six young wheat-plants in soil kept constantly wet, developed roots the total length of which measured 365 mm. each, on the average, and almost devoid of root-hairs.

Six similar plants in soil only moderately moist, averaged 668 mm., and were well furnished (though not densely covered) with root-hairs.

Six similar plants in soil which would be termed dry, averaged 371 mm., but were densely covered with rich crops of root-hairs.

Further researches have shown that the conditions which rule the development of the root-system and root-hairs in the soil are very complex, and not always easy to trace. The most general statements we can make are the following:

There is an optimum degree of moisture in the soil which promotes the maximum develop-

ment of root-hairs. If the soil is too wet they are not developed.

These facts are of importance as correlated with the ease or difficulty experienced by the roots in obtaining water, and plants such as our ordinary agricultural plants show this very distinctly.

Although, as shown in the experiments with wheat, the short roots in dry soil were more densely covered with root-hairs than the much longer roots in moderately moist soil, subsequent closer investigation shows that the total quantity and area of root-hairs is less in the former case than in the latter.

The greatest number of root-hairs are developed on roots which are growing at their best: too much moisture may prevent the formation of root-hairs: too little may induce dense growths of root-hairs locally, but the total number is reduced.

Another set of events which exerts influence on the development of root-hairs is the composition of the dilute solution—water containing dissolved salts—which surrounds them in the soil.

Thus, Schwarz found that when similar oat and wheat plants were grown with their roots in solutions of various salts, the results differed as follows:

Oats in a 15 per cent. solution of calcium chloride developed no root-hairs, though they formed in a 5 per cent. solution, and were very numerous in a 0.5 per cent. solution, or in water alone. In a 10 per cent. nutritive solution the

plants developed no root-hairs, though they were abundant in a 1 per cent. solution.

Wheat plants with their roots in a 1·5 per cent. solution of potassium nitrate bore no root-hairs, but they were numerous in a 2 per cent. solution of the same salt.

These are extreme cases, for, although the roots were not killed, they were strongly inhibited in their growth by the more concentrated solutions. However, experiments of this kind at least bring vividly before us what variations are possible, and suggest that similar events on a smaller scale may occur in a soil which yields large quantities of soluble substances, *e.g.* when freshly manured. Obviously these facts have a practical significance as regards kind of soil, drainage, season (*e.g.* drought or wet), etc.

But there are other factors which rule the development of root-hairs, and some experiments by Lesage show that the correlations between the development of root-hairs and roots are probably much more complex than had been suspected; for he finds that if the lateral rootlets of a Bean, in a water culture, are suppressed, the main rootlet develops numerous and very long hairs to compensate the loss in surface, a matter of obvious importance in the discussion of cases where roots have been injured in the soil.

Before proceeding further it is necessary to look a little more closely into the structure of a single hair.

It is a tubular prolongation of a single cell of the external covering of the young root, usually about 1 to 3 mm. in length, and 0.01 to 0.10 mm. in diameter. In special cases the root-hairs of some water plants may reach 5 to 18 mm. in length, but of course I am referring to the ordinary land plants of agriculture and forestry. This tubular prolongation is closed and rounded off at the distal free end, and opens at the proximal end into the cell of which it is a protrusion.

The whole structure is bounded by an extremely delicate and elastic wall of cellulose, which Frank says is of special composition, almost too thin to measure in many cases, but often somewhere near 0.005 to 0.001 mm. in thickness. This thin membrane is remarkably permeable by water, or dilute solutions, as is shown by the rapidity with which a root-hair collapses if exposed to evaporation, or with which dense solutions abstract water from it, or with which solutions may be seen to penetrate it under the microscope.

Overlying the thin cell-wall proper, on the outside, is a thin gelatinous layer, a product of alteration of the outermost lamellæ of the former.

Closely lining the proper cell-wall on the inside, is an extremely thin layer of living protoplasm, and somewhere in this protoplasm is a distinct cell-nucleus.

The interior of the tube is filled with cell-sap, and it is the osmotic pressure of this cell-sap which keeps the whole living instrument tense and

rigid, and the thin protoplasmic film close pressed against the cellulose cell-wall.

Nothing whatever can pass into the cell-sap, or out from it, without traversing both the lining of living protoplasm and the cell-wall.

If we gently pull a living root, of wheat, pea, mustard, etc., from a normal soil, we find particles of soil so closely adherent to the root-hairs that they cannot all be washed off without tearing the hairs: the root-hairs establish relations of contact with these particles, so close that they are cemented to the solid surfaces by means of the gelatinous layer already referred to. This peculiarity has the following consequences. In the first place, the enormous holdfast, ensured by the millions of points of adherence, enables the plant to withstand even powerful lever actions from above, and provides fixed points against which the root-tips can work as they drive deeper into the soil. In the second place, the intimate contact of the root-hairs and particles of soil, ensures that the films of water held by surface-action on the soil-particles and root-hairs shall be in continuity with the water saturating the cell-walls of the latter, and therefore with the protoplasm and cell-sap in their interior. The importance of this at periods when the soil is "dry" will be obvious, when we reflect that no soil is ever naturally so dry that surface-films of water are absent from the particles.

The fact that the root-hair contains living protoplasm, enables us to understand to a certain extent the results of the following experiments.

If we have a leafy and healthy plant, with roots, bearing numerous root-hairs, properly established in suitably moist soil in the pot, the roots cease to absorb water if the temperature of the soil falls below a certain minimum, though they recommence to do so if the temperature is raised again: this has nothing to do with the temperature of the upper parts of the plant, or of the air, and the latter may be so high that the plant rapidly droops from loss of water at the leaves, which is not being compensated owing to the inactivity of the roots.

Similarly we may have the air so cold, at a time when the soil is warm enough to keep the root-hairs actively at work, that the plant becomes surcharged with water, which escapes from the leaves like drops of dew. The temperatures necessary to cause these disturbances in the action of the living root-hairs vary for different plants, and even for different varieties of the same species.

Similar arrestation of the functions of the roots may be brought about by removing the oxygen from the soil around the root-hairs, and replacing it by carbon-dioxide, or the vapour of chloroform. If not kept too long in such a condition, the plant recovers rapidly on admitting atmospheric oxygen, which is always present in a normal well-drained soil both as gas in the capillary interspaces, and dissolved in the water on the surfaces of the particles. If the access of oxygen is delayed, however, as often happens in rainy seasons and in

wet soils, the root-hairs are killed, and rot sets in. A good instance of this has lately been given by Heinricher in the case of potatoes.

Notes on Chapter V.

For the further pursuit of this subject the reader should consult Sachs' *Lectures*, II. and XV.; Sorauer, *A Popular Treatise on the Physiology of Plants*, 1895, chapters II. and IV., and Pfeffer's *Physiology*, pp. 149-163. The principal paper on root-hairs referred to in the text is Schwarz, "Die Wurzelhaare der Pflanzen," in *Unters. aus dem bot. Inst. zu Würzburg*, I. Heft 2, 1883, p. 140, where a very exhaustive account of these organs will be found.

CHAPTER VI.

THE FUNCTIONS OF ROOT-HAIRS.

Excretions from root-hairs—Osmotic phenomena—Turgescence—Plasmolysis—Control of the protoplasm in absorption, etc. Selective absorption.

We see then that the root-hairs are the active living instruments in absorbing the water (containing small quantities of dissolved substances) of the soil.

If the living root-hairs are so numerous and so active, however, a natural inference is that they must exert some influence on the composition or arrangement of their environment. All the teachings of modern physiology go to show that such a living cell as I have sketched cannot carry on its life, brief though it be—the root-hairs are active for about four or five days—without forming substances of the nature of excreta, and we should expect some of these to pass out to the soil.

Sachs showed, in 1860, that roots growing in contact with polished marble corrode the surface

of the mineral, and Nobbe, in 1876, showed that the roots of seedlings reduce potassium permanganate, a fact which Molisch confirmed in 1887. The latter observer also proved that living root-hairs secrete substances which colour a solution of guaiacum blue, oxidise pyrogallic acid and other organic substances, and rendered it probable that they excrete some substance which inverts cane-sugar, and in some cases even small quantities of a diastatic enzyme.

Molisch also confirmed an old observation, that roots excrete carbon-dioxide; and he and Czapek showed that the root-hairs excrete acids more permanent in their nature than carbonic acid, and published a method for showing this by means of a dilute solution, slightly alkaline, of phenol-phthalein.

Molisch declared that the substances secreted by root-hairs may even be observed, dissolved in drops which ooze from the surfaces of the root-hairs.

That these root-excretions, and particularly the acids, may be of service in dissolving and rendering more available various constituents of the soil is an obvious suggestion, and it is borne out by Sachs' discovery of the corrosion of marble, and by Molisch's observation that living roots slowly corrode ivory if continuously kept in contact with it.

But a deeper insight into the physiology of these organs was only possible when the meaning of the phenomena of osmosis had been rendered

clearer by the researches of Pfeffer and De Vries in 1877.

De Vries showed that the turgescence of the living cell can be diminished, and even reduced to nothing, by placing the cell in contact with solutions of substances which attract water from the cell-sap: as the turgescence diminishes, the cell contracts, owing to the elasticity of the cell-wall, which was previously distended; if the abstraction of water continues, the living protoplasmic membrane lining the cell-wall contracts away from the latter. He then proved that no injury need accrue to the cell by this process of plasmolysis, since the turgescence can be restored by washing out the salt with a more dilute solution, or with pure water; and the cell may go on living and even growing as before. These phenomena can only be produced in cells where the protoplasmic lining is intact and alive.

Pfeffer showed that the whole matter depends on the properties of the living protoplasmic membrane, which, so long as it is alive, has the power of governing the entrance or exit of dissolved substances, but is as a rule freely permeable for water. If, then, substances with a powerful attraction for water are formed in the cell cavity, and of such a nature that the protoplasm does not permit their free diffusion to the exterior, they attract water, and hold it fast, and so set up the condition of hydrostatic pressure known as turgescence, the limit of which depends on the attainment of a state of equilibrium between the

elastic reaction of the cell-wall and the distending power of the absorbed water. When this limit is reached, water begins to filter back again through the cell-wall. Numerous researches during the last fifteen years have shown that the sap of such a living cell as the root-hair is charged with substances of various degrees of osmotic power; bodies like sugars, amides, vegetable acids and their salts, being formed by the metabolic activity of the protoplasm and accumulated there. Moreover, we now know that the salts of the vegetable acids in particular are effective, and the researches of Warburg and Palladin in 1886 have placed it beyond reasonable doubt that these acids are continually being developed and destroyed in the living cell during normal growth and respiration, and that great variations as to quantity may be brought about by alterations in the conditions of the environment—*e.g.* temperature, oxygen, etc.

If, now, we bring a solution of some salt, such as potassium nitrate, which has a powerful attraction for water, on the outside of the living root-hair, the question whether the water remains in the cell, or passes out of it, merely depends on whether the substances inside or that outside have the most powerful attraction on the water in the sap, since the protoplasm allows water to pass freely.

But the protoplasmic lining may affect the whole matter in another way; for it may allow the dissolved salt, or other substance, in the solution outside or inside the cell to pass through

it also, or it may take it up and fix it, or break it up or otherwise alter it.

More recent researches, and especially those of Pfeffer, have shown that these diosmotic properties of the living protoplasm are of the utmost importance in the whole matter of absorption of substances from the soil.

Let us suppose the following case. A root-hair, in full vigour, is allowed to bathe freely in a dilute solution of various substances, such as sugar, potassium nitrate, phosphates, sulphates and carbonates of iron, soda, lime, magnesium and others known by experiment to be harmless to its life.

Now it turns out to be by no means a foregone conclusion that all or any of the substances, even though freely soluble in the water, can pass through the protoplasm into the interior of the cell. Some may be allowed easy access, others may only be permitted to pass in small quantities, and others, again, may be absolutely refused access by the delicate living filter, so long as it is vigorously alive. Nor, as proved by numerous experimental cultures since De Saussure's time, is the entrance of a salt, etc., ruled by its indispensability or otherwise in the economy of the plant. And it is important to notice that only experiment can prove the point and determine which substances are absorbed and which refused by the root-hair.

If we now suppose the protoplasm to give rise to powerfully osmotic substances which accumulate

in the sap-vacuole, but which are not permitted free egress through the protoplasm (and the formation of such bodies will occur if the protoplasm is actively respiring), the conditions for absorption of water, with or without any dissolved salts, which the protoplasm allows to traverse it, are set up.

But the above supposed case is realised, as Pfeffer showed in 1886, when he found by a series of beautiful experiments that certain aniline dyes can accumulate in living root-hairs, and other living cells, whereas others cannot pass the living protoplasm. After accumulating for some time, the dye may either remain stored there, or may eventually diffuse out.

Pfeffer made another discovery, of equal importance, namely, that under the influence of dilute organic acids, such as citric acid, the permeability of the living protoplasm may be altered, so that it allows substances to pass which could not otherwise have traversed it. De Vries had also shown that the condition of the protoplasm affects its power of retaining the colouring matter in the sap of the Beet: so long as the protoplasm is alive, the crimson sap is retained, even when the cell is plasmolysed, but immediately it begins to die the colour escapes through it. A similar case exists when the chlorophyll-corpuscles retain their colour in living cells known to be charged with acids: so long as the protoplasm is alive and normally active the green bodies are protected.

These, and numerous other experiments of the same kind, prove that the healthy root-hair is a living instrument for taking up dilute solutions out of the soil, and holding them in the sap-cavity for a time. If killed, by frost for instance, it loses these powers.

The researches of the last ten years have also shown that a time comes when the turgid cell, if an isolated one, and if sufficient supplies of water are present, is so tightly distended that the surplus water begins to diffuse out again under the pressure proper to the hydrostatic conditions set up.

Now we arrive at a very critical point.

When the water, or dilute solution of various substances, begins to exude under pressure from the living root-hair, what is to prevent its escape into the soil? And if it thus diffuses out, where is the object of absorption?

The questions are obviously pertinent, and they may seem the more so in that the cells adjoining the root-hair on its inner side are also turgid, and possess similar properties to those of the root-hairs. To establish a condition of things which shall bring about the inward flow of the absorbed water, one of the three following cases is conceivable. (1) The cells, as we pass radially into the root, have different properties on the wall of the two sides; or (2) they are more and more greedy of water owing to some process of extraction of their water by tissues in the centre of the root; or (3) these successive series

of cells possess osmotically more powerful contents at periods coincident with the escape of the water from the now osmotically weaker root-hairs.

A little reflection will show that where we have a group of such cells as the above, all capable of absorbing water and dilute solutions and of becoming turgid, movements of the absorbed water must go on until all the cells are in equilibrium, as regards their osmotic pressures.

Now the living rootlet is just such a system, the various cells of which are in different conditions of osmotic pressure at any given time: some of these cells are old, and their protoplasm is allowing sap to filter out under pressure: others are in the height of their vigour, and their protoplasm extremely impervious to the highly osmotic sap-constituents which it itself is forming actively: others are too young to have attained their full turgescence: while others again are in stages intermediate between the above.

There is another point of importance, however, to explain some peculiarities in the absorption of these dilute solutions of salts, etc., by the root-hairs from the soil, and by cells lying deeper in the plant from these root-hairs.

It is easy to understand that if a root-hair absorbs a given substance—say calcium sulphate, for illustration—and hands it over to other cells unchanged, a time must be supposed to arrive when, the sap of all the cells being equally charged with calcium sulphate, no more could be

absorbed : the rate of absorption of this particular substance, and the quantity absorbed, up to the hypothetical point of equilibrium chosen, would then depend simply on the ease with which its molecules traversed the living protoplasmic membrane, and the degree of their solubility in the sap.

But now suppose the following new factor to come in. Suppose that calcium sulphate undergoes decomposition in some one of the internal cells of the system of absorbing cells, or that it is even merely crystallised out in such a cell, or in any other way removed from solution (*e.g.* by deposition in cell-walls). This alters the state of affairs considerably. The separation of the molecules from the sap-solution is itself a cause for the flow of more of the solution to the cell concerned, and such causes of diffusion are very common in the plant.

The importance of this principle consists in that it lies at the base of the whole question of selective absorption, application of manures, and the rotation of crops ; and those who are acquainted with the excellent analytical results of De Saussure, Boussingault, Wolff, Trinchinetti, Gödechen, etc., and the water-culture experiments of Sachs, Nobbe, and others, will understand what an illuminating effect on these points was produced by the above generalisation, which we owe especially to Pfeffer's splendid researches into the nature of osmotic phenomena.

It will now be clear, I hope, why we regard

the living root-hairs as instruments—as pieces of living machinery—for the active absorption of water, with substances dissolved in it, from the soil; and it will also be evident, I think, that no one can form a proper conception of this matter of absorption, so important in all agricultural questions, unless he pays attention to these biological phenomena. It was hopeless to expect to understand these matters merely in the light of chemical analyses of plants and soils, and one expression of this hopelessness was the belief in the power of roots to select only the substances useful to it. We now know that the expression "selective power of roots" has a totally different meaning from that implied in the minds of the last generation of agriculturalists, and it would be easy to devise experiments, with solutions of different strength, where the plant should be made to take up relatively large quantities of harmless, but useless minerals, etc., and to starve in the midst of plenty of the elements proper to its structure, simply because the former are offered in a form in which they easily traverse the protoplasm of the root-hairs, while the latter are presented in a form unsuitable for absorption. That all these matters are of importance in regard to manuring and choice of soils, etc., needs no emphasising.

These remarks, of course, do not detract from the value of good comparative chemical analyses, when viewed in the light of physiological knowledge, as I need hardly say; but they do, and

emphatically so, attack the position that such analyses alone can explain the problems of agriculture.

On the other hand, we must not rest satisfied with the suggestions so far put forward to account for the processes referred to, since it is impossible to overlook the fact that in their present form they merely afford proximate explanations, and and are too crudely mechanical for finality.

Notes on Chapter VI.

In addition to the works referred to in the last chapter, the student should consult Pfeffer's *Physiology*, pp. 86-149, and pp. 410-441. With reference to water cultures, Sachs' *Lectures*, XVII., may also be consulted. The standard work on ash constituents of plants is Wolff, *Aschen-analysen*, 1871 and 1880, an indispensable book of reference in this connection, though there are others, quoted in Pfeffer, where further literature may also be found.

CHAPTER VII.

THE BIOLOGY OF SOIL.

Soil not a dead matrix—Organic materials—The living organisms of the soil—Their activities—Their numbers and importance. Abandonment of the notion that chemical analysis can explain the problem.

It is customary to regard the soil, between the particles of which the root-hairs of plants are distributed, as if it were merely a dead matrix of smaller or larger pieces of rock, such as sand, gravel, stones, etc., and organic remains, such as bits of wood, leaves, bones, etc., with water and air in their interstices. As matter of fact, however, soil is a much more complex body than was suspected until comparatively recent times.

It is, of course, beyond the scope of this book to go into the different varieties of soils, their structure or arrangement, and the chemical nature of their constituent rocks and the débris mingled with the latter. For the same reason I must pass over the curious properties of soils in relation to

the solutions they yield to water in contact, the manner in which they retain some of these solutions and allow others to pass easily, and the remarkable double decompositions which go on in them. Moreover, I must assume as known the chief physical properties of ordinary soils with respect to the phenomena of capillarity, absorption of heat, action of frost, and so forth.

But all ideas as to the nature of soil based merely on the study of its chemistry and physics are misleading, and it is in just the establishment of this truth that modern discoveries in Agricultural and Forest Botany have played so important a part.

From the facts that organic débris is found chiefly at the surface of the earth, and that the smallest particles are held in suspension by the water near the surface, it is comprehensible why such organic remains abound in the upper parts of the soil, where the rootlets with their absorbing root-hairs are also found, because they must have oxygen. The rule is, therefore, that an ordinary soil consists of upper strata, rich in organic materials and in oxygen, and a subsoil, poorer in these substances.

Among these organic materials are countless myriads of living beings, especially fungi and bacteria, which require oxygen and organic materials for their subsistence, and it depends on the open or close, moderately moist or damp, warm or cold nature of the soil, and on some obviously connected factors, how far down these aërobic organisms can thrive. As we go deeper down they

become fewer and fewer, and gradually disappear, and (neglecting certain anaërobic bacteria of putrefaction) they are rarely found in marked abundance more than a few inches below the surface soil.

These aërobic fungi and bacteria are the great agents of continued fertility of a soil, and it is they which, living and multiplying in the moist and well-aerated warm interstices of a rich open soil, carry out the useful destruction of organic matter, breaking it up into mineral and gaseous bodies, which are then dissolved in the water bathing the root-hairs or escape into the atmosphere. In this work of destruction they are aided by the oxygen of the air and the solar heat: their own fermentative action is also accompanied by a marked rise of temperature, and the carbon-dioxide and other products of their activity all go to complicate the chemical changes going on in the soil around the roots.

Duclaux has calculated that *Aspergillus niger*, a common mould fungus, can break down organic substances, such as carbohydrates, at such a rate that a metre cube of the fungus would decompose more than 3000 kilogr. of starch in a year, and this may serve as an example giving some idea of the possibilities in soil.

Analyses of waters containing large quantities of organic matter, as they enter such open soils as those referred to, compared with the drainage water after passing through the upper strata, show that the carbonaceous and nitrogenous materials are broken down to more or less completely

oxidised simpler compounds, and that the following chief changes result. The ammonia and some other nitrogenous bodies remain behind in the soil, as also do the phosphoric acid and much of the potash ; whereas large quantities of nitric and nitrous acids, together with much sulphuric acid, chlorides, and calcium salts pass away in the drainage. These facts are obviously highly important in agriculture.

Experiments on sewage farms have shown also that the upper soil retains most of the bacteria of the sewage. Koch found at Osmont, near Berlin, that whereas the different sewage waters contained numbers so enormous that each cubic centimeter probably held 38,000,000 germs, the different drainage waters held only 87,000 per c.cm. ; and the whole process of water-filtration through sandy soils depends on these well-known facts.

Recent experiments in connection with soil-filtration, however, bring out the further facts that the oxidations which organic matters undergo in the soil—and without which they are useless to the higher plants—are enormously enfeebled if the upper layers of soil are sterilised, so as to deprive them of the myriads of aërobic bacteria, fungi and yeasts which they normally contain, and there can no longer be any doubt as to the importance of the biology of the soil in connection with the preparation of materials suitable for absorption in solution by the root-hairs of agricultural and other plants.

The researches of the last ten years have

brought to light a long list of forms, comprising yeasts, such as Hansen's *Saccharomyces apiculatus*, fungi and bacteria which live and grow in the soil, finding their water and food supplies in the interstices, and under conditions which we now know to be very diverse. They are usually more numerous, in species and individuals, in cultivated farm and garden soils than in woods, prairies, and untilled lands; but the geological nature of the strata, the closeness and otherwise of the soil, its damp or dry character and its average temperature (which depends on many things besides latitude or altitude) and other factors co-operate to rule their distribution and numbers. The fact that cultivated land is so well supplied with manures, air, etc., is of great importance in relation to their relative abundance there, and it is extremely probable that the use of artificial manures lessens their numbers considerably as compared with land on which stable and other animal manures are employed.

A list of the soil-bacteria which have been isolated and more or less carefully cultivated and examined would comprise about fifty species; but it is certain that, as at present classified and named, many more species are to be discovered in any ordinary soil.

The fungi are apparently even more numerous than the bacteria, and we may rest satisfied for the present with the general statement that the life-actions of the myriads of individuals of these organisms in the soil completely alter the question

of soil-water as understood by the last generation of agriculturalists.

But there is another aspect of this question of soil-organisms which has grown in importance of late to such an extent that we are more than ever justified in regarding the biology of soil as far more vital to the interests of the plant than its physical or chemical properties. With many of the fungi in the soil the roots of plants have to compete—just as plant competes with plant—for water, salts, and other food-materials. The toad-stools which are so conspicuous in fields and forests spring from mycelia which ramify in the ground, and are busily breaking down the remains of other organisms, and just such fungi are known to store up relatively large quantities of salts of potassium and phosphorus—the very salts which are so valuable to crops and occur so sparingly in most soils, but which the extensively spread fungus mycelia can gradually accumulate. Some of these fungi, moreover, are more active in their antagonism, and actually attack and pierce the roots as destructive parasites, but I pass these by for the present, as they form the subject for further consideration when we come to the diseases of plants.

It is obvious that the competition of fungi with root-hairs for mineral salts, oxygen, etc., may be at times acute, and it is extremely probable that cases of so-called sterility of soil, where a particular soil is found unsuitable for a crop, may sometimes be due to this over-competition.

The researches of recent years, however, and especially those of Frank, Winogradsky, Hellriegel, and Stahl, have brought to light a series of relationships between certain of these soil-organisms and the higher plants which place the matter of soil-biology in quite new lights.

On the one hand it has been discovered that groups of bacteria are the active agents in bringing about the destruction of organic nitrogenous matter with the formation of ammonia, in oxidising this ammonia to nitrous and to nitric acids, which combine with bases in the soil to form the corresponding salts; while, on the other hand, other forms can decompose the nitrates and reduce them to nitrites, or set free ammonia or even nitrogen from them. Moreover, there are certain species which can fix the free nitrogen of the atmosphere, and start the cycle of up-building of this inert element into the complex higher compounds we term organic. It is impossible to over-estimate the importance of these processes of nitrification and denitrification going on in the soil about the root-hairs of the higher plants.

But, in addition to this circulation of nitrogen in the soil, it turns out that the life-actions of bacteria, and not mere chemical decompositions, are largely responsible for the circulation of carbon, of iron, of sulphur and other elements formed from the decomposition—also by bacterial and fungal agency—of animal and vegetable remains in the soil.

Even more startling are the biological relations

in the soil between the absorbing roots of the higher plants and some of these bacteria and fungi, for it has now been established beyond all doubt that certain fungi enter the living roots and there flourish not as mere destructive parasites, but as messmates not only tolerated by the plant, but even indispensable to its welfare. It is probable that nearly half the plants of our fields, moors, and forests entertain such fungi in their root-tissues. The curious, and long-known nodules on the roots of leguminous plants—peas, beans, clover, etc.—are filled with bacteria which enable these plants to avail themselves of the free nitrogen of the air, and so enrich the soil with nitrogenous substances.

The roots of most forest trees, orchids, and plants of the moorlands, meadows and marshes are similarly occupied by fungi, which in some way convey salts—probably especially phosphates and potassium compounds—to the plant in return for the small tax of organic carbon-compounds it exacts from the latter. In some cases at any rate, as Bernard has lately shown, the very existence of the plant depends on its seedling roots obtaining this advantageous attachment and co-operation (symbiosis) of the fungus immediately on germination.

These remarks must suffice to illustrate this part of my subject, and to emphasise the statement that the question whether a given plant can be grown in a given soil, is by no means one of simply the physical and chemical constitution of the latter. The plant will have to run the gauntlet of a long series of vicissitudes brought

about by the presence or absence, relative proportions and vigour, and specific nature of the organisms in the soil at its roots, and it is easy to see that many cases of disease may be due to the absence of advantageous bacteria or fungi, or to circumstances which disfavour their life, as well as to the predominance of competing organisms.

It will now be evident that the old points of view must be abandoned, and with them, especially, the widely prevalent notion that chemical analyses of the plant and soil can explain the real problems of agriculture.

It was of course an enormous advance in the science when, thanks to the splendid labours of the chemists, at the end of the last century and the beginning of this, we obtained that preliminary knowledge of the constitution of the air, and of the composition of the water, acids and salts, etc., which plants require for their food-materials and life-processes. Much was gained by De Saussure's establishment of the fact of oxygen respiration, though we now understand by the term something very different from, and much more complex than, what he understood by it, as, also, much had been gained by the previously acquired knowledge of the gas-exchanges in carbon-assimilation: nor must we forget the services of those who proved, by laborious analyses, continued for long periods, what chemical compounds are found in the tissues of plants, and in the soils at their roots and the atmosphere which surrounded them. We must also remember many other con-

tributions which have been furnished, and are still being furnished by the chemist; and I for one hope that his labours will continue to go hand in hand with those of the physiologist.

But, when all due honour is paid to the scientific chemist, it must still be allowed that his problems are different from the real problems of agriculture. To take one set of instances alone. The chemist can analyse a given soil or a given manure, and can even go a long way towards making them, but his analyses do not tell us what conditions are necessary in order that their ingredients may be presented to the roots so as to be absorbed and become built up into the plant. Chemistry told us that carbon was fixed from the air, but physiological experiments determined how this meant the synthesis of certain definite carbohydrates—this, too, in the face of the powerful authority of the chemist Liebig, who supposed that the vegetable acids were the results of the assimilation of carbon. Wolff, De Saussure, and other chemists have done yeoman service in showing that different plants, growing in the same soil, contain different proportions of mineral substances; but it was by means of water-cultures, and other physiological researches, such as those of Pfeffer on osmotic phenomena and of Schwarz and Molisch on root-hairs, that the puzzling question of selective absorption, by means of the living root-hairs, came into the arena of our knowledge.

In every case—and, as already said, I am not undervaluing the work done—the chemist has left

us only on the threshold of the real problem. He has stood outside the factory in which the real work we want to know about is being carried on, and has told us of so many tons of this material being carried in at the gates, and of so many tons of that coming out ; he has even burnt down the factory, and all its contents and machinery, and has then told us how many tons of the various materials were there at the time ; but this is not what we want, valuable as the information is, and still more will be. What we want, and what we expect to obtain, is more information regarding what is done with the materials in the factory: what machinery they are put into, and how they are put in : what stages they go through, and how the stages follow one another : what wear and tear has to be endured, and how we can step in and stop the working of the machine for our own benefit at the best possible time.

The physiologist proceeds empirically, by experimenting with the living machinery. He recognises the parts and their structure, and tries to find out what they are doing : he knows that the laws of physics and chemistry cannot be traversed, but he sees these laws at work under special and very complex and peculiar conditions. He therefore, as the results of his experiments, sets new questions —or old questions under new conditions, if you like—and undoubtedly wants the help of both chemist and physicist ; or, if it is preferred, the chemist and physicist may attack the problems, but they must familiarise themselves with the

peculiar mechanism of the organism concerned, and cannot hope to attain success without experimenting with it. I confess it seems to me as reasonable to look upon scientific agriculture as a branch chiefly of chemistry as it would be to look upon horse-breeding or pigeon-rearing from the same point of view; and why the professed chemist's advice is regarded as so comforting and final in the one case and not in the other is one of those mysteries which seem inherent in human nature.

The central point in agriculture is the plant: get the most out of it—the energy-winning machine which alone can keep the animals and everything else connected with the farm going—and all the rest follows. The old agriculture has taken a gloomy view of things, and especially on account of a large variable which it blames for many ills, namely, the season or climate. Perhaps the old agriculture has not sufficiently recognised that Nature grows plants in accordance with the fact that variation is not peculiar to the weather: if the seasons vary, so do fruit and other produce and the plants which yield them; and since man cannot hope to control the one variable, possibly relief will be found in doing more, within his limits, towards controlling others.

In any case he cannot hope to succeed without study of the physiology of the plant.

Notes to Chapter VII.

An admirable short account of soil in its relation to root-hairs is given in Sachs' *Lectures*, XV.; but for a more exhaustive

treatment of the subject of soil the reader is referred to King, *The Soil* (Wisconsin, 1895), or Warrington, *Lectures on the Physical Properties of Soil* (Oxford, 1900); Larbalétrier, *L'Agriculture* (Paris, 1888), chapters II. and III. There is also a very good account in Bailey, *The Principles of Agriculture* (London, 1898), chapters I.-III.

With reference to the organisms in soils and the decompositions they bring about, the student should consult Kramer, *Die Bakteriologie in ihren Beziehungen zur Landwirthschaft* (Wien, 1890), and Lafar, *Technical Mycology* (Engl. edition, 1898), sections V., VIII., and IX.

CHAPTER VIII.

HYBRIDISATION AND SELECTION.

The crossing of varieties of wheat, etc.—The essentials of fertilisation—Rimpau's experiments—Hybrids and selected varieties.

In the more hopeful view of the case which the new agriculture will have to take, it will recognise the physiological truth that since the living plant is the important and variable machine which constructs the produce looked for, and since that machine will work best in proportion as its needs are properly satisfied; therefore in cases where the needs of a given type of the machine cannot be efficiently provided for, it will be well to select some other type which will take what supplies and conditions can be offered. Of course, this is already recognised to a certain extent, as is implied in the practices of "rotation of crops," selection of "pedigree wheats" and mixtures of "pasture grasses," and in decisions as to the quality of land according to the kinds of weeds found on it, and

so forth; but I am convinced that the agriculturist of the future—and the same applies to the horticulturist, planter and forester—will have to concern himself more systematically with the working and the variability of the plant, and particularly with what Darwin termed Variation under Domestication, than has always been the custom in the past. The subject of the plasticity of cultivated plants, and especially of hybrids, is in one sense an old one; but much work is being done which proves, as such work is apt to do, that very much more may be done by well-planned experiments on the selection of new varieties raised by hybridising and cultivation.

In illustration of this point, a short summary of some of the results of crossing different species of wheat, barley, oats, peas, beet, etc., may serve to show what has been gained and what may be hoped for in these directions. It should be stated that much has been done and is being done in this country as well as abroad, as witness English varieties of corn, peas, and potatoes, and the recent experiments on crossing various kinds of maize in America.

The hybridiser grows his cereals, etc., in pots until ready for crossing, and then takes them into the laboratory, removes the weaker spikelets, and takes out the young stamens from the flowers left on the plant. The female plant is then ready, and the flowers covered with paper caps. The pollen, obtained by a clean wet brush from the plant chosen as the father, is then carefully placed in

position on the stigmas, and the caps replaced. The pollination is repeated occasionally, and care taken that no uncrossed flowers develop later. In this way a few seeds or grains are got to start with.

This would be the place to introduce an account of the enormous advances made by the botanists of the last decade or two in the study of the microscopic phenomena of fertilisation. Without going into details—which would more than occupy all the space at command—I may recall the discoveries of Strasburger and his pupils, and of Guignard, which have supplemented the earlier discoveries of De Bary, Cohn, and Hofmeister, by establishing the facts that the essential point in fertilisation is the fusion of two nuclei, and the bringing together in the fused mass of two extremely minute thread-like coiled bodies, the so-called chromatosomes or filaments, one of which is derived from the male and the other from the female parent. The particulars as to the marvellous adaptations to secure the union of these two infinitesimally minute threads, their behaviour immediately before and after union, and many other points must be passed over, as I have only space to emphasise the one crowning discovery that these tiny filaments of nuclear substance are the material carriers of all the hereditary properties of the parents to the young plant which their union initiates.

It must not be supposed that the above statements are based on any meagre foundation of facts. The attraction of the fusing nucleated masses had been demonstrated over and over

again by Tulasne, De Bary, Strasburger and others; but Pfeffer brought the matter to a crisis by discovering the attractive (chemotactic) substance emitted in given cases, and by collecting the fertilising bodies by its means into artificial tubes.

The fusion of the nucleated bodies in the sexual act was observed by Strasburger in the living plant a few years ago, and numerous later observers have confirmed it. Meanwhile all the stages of approach and contact of the essential filaments of the nuclear substance have been traced, as also all the stages of the transference of half of each filament, male and female, into each of the first two cells of the very young embryo-plant.

Moreover, the essentials are found to be the same in the animal kingdom also, and the bearing of all these discoveries on the phenomena of reproduction, variation, and heredity in living organisms has been and is of the highest importance, for they support, control, explain and correct so many of the splendid results of Knight, Kölreuter, Sprengel, Hildebrand and Hermann Müller, and in every direction throw side-lights into the crevices of that magnificent structure, the theory of Natural Selection, erected for all time by our countryman, Charles Darwin.

To return now to experiments on crossing. It is found that the first products of the crossing appear exactly alike; they may have characters intermediate between those of the father and mother, or they may resemble one more than the

other, but all the seeds of the same cross do it in the same way.

On then sowing the seeds of the plants produced from this first cross, variations begin to appear. Most of the progeny revert to one or other of the parent forms, others show all conceivable combinations of their characters, and a few may give rise to entirely new characters. In succeeding generations the reversions are preponderant, and, supposing no care is taken to prevent it, the whole of the offspring gradually go back to the ancestral type.

Some important consequences result, however, if systematic care is brought to bear on the matter. This tendency to variation in the second generation of crossed plants has often been noted, and it bears out very distinctly the conclusions to which Darwin came.

The hybridiser takes advantage of this variation, as others have done, to select some forms and rigidly suppress others, in order to obtain well-marked varieties of the plants he experiments with. In illustration, I may take the following from Rimpau's account of his experiments on crossing wheat: By crossing a white English long-eared, dense wheat, and celebrated as a heavy cropper, with a red, looser German wheat, remarkable for its resistance to winter cold, Rimpau hoped to obtain a variety uniting both the above qualities. As regards the property of resistance, he failed, and he eventually gave up the attempts in face of the advantages offered by the

so-called *Square-heads*, which then came into the market. His experiments, even with the above varieties, are worth noting, however, for they show how promising the results of carefully conducted crossing and selection may be.

The crossing was done in 1875, in both directions. In 1876 the few grains obtained were found to yield plants almost all alike, with the long loose ear of the German parent, but the paler colour of the English wheat.

In 1877 the plants, obtained by sowing the finest grains, were found to consist of pure white, pure red, and of forms which appeared to vary and revert in all possible degrees as regards colour, density, and other characters intermediate between these.

By carefully separating the closest and densest white wheats from the closest and densest red ones, he got in 1878 a large number of each coming nearer to the type sown than did the mongrel forms intermingled with them: these reversions and intermediate forms were then rigidly eliminated, and only the deepest coloured and densest red and white forms again sown.

In 1879 these two chosen varieties were constant, so far as concerned those selected from the crossing of female English white with male German red wheat, and the following year proved the constancy of the red variety in the reciprocal cross. In 1886 all four varieties—*i.e.* the two reds and the two whites of both the crossings—had become constant.

Still more instructive are the results of the cross between the same white English non-bearded wheat and a red German bearded wheat.

The first results of the crossing in 1875 showed the loose ear of the German mother, but was paler in colour; while the influence of the English father was shown by the absence of beard.

From the reversions and mixtures of the mongrels showing reminiscences of the parents in all degrees in 1877, rigid selections and re-sowings were made as before, and Rimpau eventually got four very distinct varieties, two red and two white, a bearded and a beardless form of each, and these were declared fixed and constant in 1879-1882.

Passing over many similar results, and merely noting a very successful variety got from a cross between a very early ripening loose red American wheat and the dense heavy cropping English Square-head—the crossed variety which has proved very suitable for certain light soils and dry climates on the Continent, which demand very rapid ripening, and are therefore of great physiological and technical interest—I must pass on to note the curious result of the successful hybridisation of wheat and rye. This cross has been effected several times, and first in this country according to reports from Edinburgh (1875), New York (1886), and elsewhere, and Rimpau's careful experiments seem to leave no doubt on the matter.

First I must remind you that wheat (*Triticum*) differs from rye (*Secale*) in several marked characters, such as the breadth and shape of the glumes, the number of flowers in the spikelet, etc.; and that the cultivated rye differs from cultivated wheats in the characters of the straw, in having long ears, and in its flowering glumes remaining widely divaricated for some days when in flower.

In 1888 Rimpau removed the young stamens from the German wheat referred to, and pollinated the stigmas with pollen from a long-eared rye. Four sound grains were obtained, looking like wheat-grains.

The history of one of these grains was as follows: In 1889 it yielded ears which were peculiarly narrow and long, and its stalks were also much longer than the wheat: the flowers remained exposed, with widely open paleae, for several days, and the grains were very peculiar, though wheat-like.

Fifteen of the best grains were selected, and in 1890 three of the resulting plants proved to be a wheat of the Square-head type and one quite sterile. The others retained the elongated, narrow, brownish-red ears, the flowering glumes again opening wide for some days. This last is a characteristic of rye, but not of wheat.

A long series of natural hybrids of wheat, barley, and oats are also described and discussed by Rimpau, as well as artificial crosses—some very remarkable—of barleys, but they must be passed over here.

Peas rarely become hybridised naturally. According to Darwin, H. Müller, and Focke, the flowers are little visited by insects in our countries, though the mechanism points to their adaptation for pollination by large bees.

Rimpau confirms Darwin, H. Müller, and Ogle as to the self-fertilisation of our cultivated peas. Nevertheless, as is well known, marked varieties have been obtained by artificial crossing by Gärtner, Knight, Laxton, and others, especially in this country.

At the same time experiments show that while it is very easy to obtain artificial hybrids of such plants, and there is no fear of natural inter-crossing, the forms are remarkably unstable as yet. Similarly unsatisfactory results were obtained with beet. As experiments are still going on, however, we may expect to hear more about these and other results.

It is probable, from recent experiments by De Vries, Correns, and others, that a remarkable regularity, expressed by Mendel in the form of a law, obtains in the variations which result from hybridising.

In considering these illustrative cases, it is necessary to thoroughly apprehend that two procedures are involved. In the first place we have the cross-pollination leading to the formation of the hybrid plant by cross-fertilisation. But experience shows that this would lead to very uncertain results if the plant-breeder did not supplement them by the second and extremely

important process of rigid selection—*i.e.* by choosing the best of the progeny and breeding from them apart from the parent-forms, and gradually intensifying, as it were, the variations in certain directions which have been started by the crossing.

It is by selection, careful culture, and repeated selection that so much has been done in obtaining the innumerable new varieties of roses, sweet-peas, orchids, orchard fruits, cereals, grapes, strawberries, melons, tomatoes, early potatoes, etc., brought forward by numerous breeders of plants in all countries, as will readily be understood if reference be made to the work of Hays and Webber in America; Saunders in Canada; Garton, Sutton, Veitch, Bateson, and others in this country.

Nor is it necessary that the new materials for selection to work upon should be started by hybridisation. Grafting, change of conditions, and even variations so vaguely understood that we term them "spontaneous," may supply the starting-points for changes in the characters of plants, so remarkable after intensification by breeding that people find it difficult to believe they can have come from one stock.

Here, however, I must conclude, merely remarking that the above sketch is a mere outline of the subjects modern agriculture and horticulture concern themselves with. There are hundreds of problems connected with the germination of seeds, on which valuable recent work has been done by Klebs, Green, Horace Brown, and others; with

the resistance of seeds and seedlings to high and low temperatures, a subject opened out by Sachs, Kny, De Vries, Krasan, Just, Höhnel, Dewar, Dyer, and others; with the conditions of vegetation which affect the various functions of growth, respiration, assimilation, transpiration, and so forth, on which I cannot even touch in these pages.

Meanwhile I hope I have succeeded in impressing upon you the grand fact that the plant is a living and very complex engine, driven by the radiant energy of the sun, and capable of doing work thereby, and this just as truly as any heat-engine is driven by chemical energy gained by means of the sun's rays, or as a water-mill is driven by power which must be referred to the energy of potential in the head of water placed in position by the sun's work in evaporation. Fundamentally the whole of life and work on our planet is to be referred to the one great source of energy which renders possible the establishment of differences of potential.

This machine, then, doing work in various ways, adapts itself—or goes to the wall—to the conditions of its work among competing organisms or opposing circumstances. Curiously enough, while in some cases it suffers from the competition, in others it is benefited by its life-actions fitting in between those of other organisms, which in their turn supplement it. In other words new types of this engine, capable of doing the work in various ways, are obtainable; some

are good types for the conditions afforded, others are bad ones.

Examples of both will occur in the further exposition of the subject.

Man's position in regard to the struggle is that of an intelligent being who steps in at certain stages and protects, fosters, and in every way favours the agricultural plant—the living machine—and sees that every opportunity is given it to do its best work in the best way—from his points of view!

Notes to Chapter VIII.

The foundation of any course of reading on hybridisation and selection should be Darwin's *Effects of Cross and Self-Fertilisation in the Vegetable Kingdom*, which, with his books *On the Origin of Species by means of Natural Selection* and *The Variation of Animals and Plants under Domestication*, will prepare the student for the long course of reading necessary for a full appreciation of what has been done in this department of science.

From the numerous works which followed these I should select Bailey's *Survival of the Unlike*, London, 1896, and *Evolution of our Native Fruits*, New York, 1898, as especially useful for the reader of this book, to which may also be added *Plant Breeding*, New York, 1896, by the same author, as giving numerous facts and practical directions of value. Further, the "Hybrid Conference Report," *Journ. Roy. Hort. Soc.*, 1900, abounds in facts and information. Rimpau, *Landw. Jahrb.*, vol. xx., 1891, p. 239. The student who wishes to get towards the root of the matter will hardly be able to dispense with Strasburger's *Neue Untersuchungen über die Befruchtungsvorgang bei den Phanerogamen*, Jena, 1884. An interesting summary of recent work on *Xenia* and "double fertilisation" will be

found in *Bull. No. 22, U.S. Dept. of Agric.*, 1900. See also *Nature*, Mar. 15, 1900, p. 470.

If he wishes to explore the vast region of controversial literature that opens up from these points, and which is far beyond the purpose of this book, he may consult the literature collected in Kassowitz' *Allgemeine Biologie*, Wien, 1899, B. II., and the references in the works quoted; also, Strasburger, "The Periodic Reduction of Chromosomes in Living Organisms," *Ann. Bot.*, viii., 1894, p. 281. For "Mendel's Law," see Correns in *Ber. d. deutsch. bot. Gesellsch.*, vol. xviii., 1900, p. 158.

PART II.

DISEASE IN PLANTS.

CHAPTER IX.

PHYTOPATHOLOGY. DERIVATION AND MEANING.

History. References in the Bible—Greeks and Romans—Shakespeare—Rouen law—Superstitions—Malpighi and Grew—Hales—Unger—Berkeley—De Bary, etc. Physiology and Biology—Diagnosis—Etiology—Therapeutics. Study of causes.

PHYTOPATHOLOGY, from Greek words which signify to treat of diseases of plants, comprises what is known of the symptoms, course, and causes of the diseases which threaten the lives of plants, or bring about injuries and abnormalities of structure. As a distinct and systematised branch of botany it is a modern study, the history of which only dates from about 1850, though the subject had been treated more or less disjointedly by several authors during the preceding century, and isolated records of diseased crops, fruit-trees, etc., exist far back in the history of Europe. The existence of mildews and blights on cereals indeed

was observed and recorded by the writers of the older books of the Bible, half a dozen references to such blights being found in the Old Testament, as well as others to blasted fig trees, etc., in the New Testament. Aristotle, about 350 B.C., noticed the epidemic nature of wheat-rust. The Greeks and Romans were so well acquainted with such diseases that their philosophers speculated very shrewdly as to causes, while the people dedicated such pests to special gods. As regards the Middle Ages, we know little beyond the fact that blights and mildews existed, but Shakespeare's reference in *King Lear* (Act III., Sc. 4) leaves no doubt as to his acquaintance with mildew in the 17th century, and other authorities bear out the same. Even the law took cognisance of the danger of wheat-rust in 1660 in Rouen (Loverdo). Prior to the 18th century, however, only meagre notes on the subject occur scattered here and there among other matters, and much superstition existed then and later regarding these as other diseases.

Malpighi, in 1679, gave excellent figures of leaves rolled by insects and of numerous galls, the true nature of which he practically discovered by observing the insect piercing the tissues; previous observers—Pliny knew that flies emerge from galls, but thought the latter grew spontaneously—having nothing but superstitions and conjectures to offer. Grew, in 1682, also gave a capital figure and description of a leaf mined by "a small flat insect . . . which neither ranging in breadth nor striking deep into the leaf, eats so much only

as lies just before it, and so runs scudding along betwixt the skin and the pulp of the leaf, leaving a whitish streak behind it, where the skin is now loose, as the measure of its voyage"—a by no means inadequate description of the injury and its cause.

During the eighteenth century several academic treatises or dissertations dealing with diseases of plants appeared.

But as a rule we only find disjointed notes. Hales (1727-33) discusses the rotting of wounds, canker, and a few other matters, but much had to be done with the microscope ere any substantial progress could be made.

With the nineteenth century, and the founding of the modern theories of nutrition by Ingenhousz, Priestley, and De Saussure, we find a new era started. As the discoveries of the microscopists continued to build up our knowledge of the anatomy of plants and began to elucidate the biology of the fungi and other cryptogams, while the chemists and physiologists laid the foundations of our modern science of plant life, it gradually became possible to tabulate and classify plant diseases, and discuss their symptoms and causes in a more scientific manner. Even in 1833, however, Turpin, and a far better observer, Unger, regarded parasitic fungi as due to diseased outgrowths of chlorophyll-corpuscles and parenchyma cells, views shared by Meyen (1837) and Schleiden (1846). We may pass over the various treatises of Wiegmann (1839), Meyen (1841), Raspail

(1846), Kühn (1859), and a number of other works of the period, merely referring with emphasis to Berkeley's admirable papers in the *Gardener's Chronicle* (1854) for a summary of what was then known. All these works antedate De Bary's *Morphologie und Physiologie der Pilze, etc.* (1866), in which he brought together the results of his researches during the decade, proving the real nature of parasitic diseases and infection as worked out by experiments between 1853 and 1863.

This work put the whole subject of parasitic diseases of plants and animals on a new footing, and paved the way for the modern treatment of plant pathology as elaborated in the treatises of Frank (1880 and 1895), Sorauer (1886), Kirchner (1890), and others, to which the reader is referred for further details. I will merely quote the following passage from Raspail's *Histoire Naturelle de la Santé et de la Maladie*, 1846 (vol. ii., p. 176), in illustration of the views entertained by high authorities just prior to De Bary's work: "L'insecte qui produit les *erineum*, *uredo*, *æcidium*, *xyloma*, *puccinia*, n'est donc plus pour nous un insecte inconnu, mais un *acarus* (grise), un *aphis* (puceron) ou un *thrips*, qui produit au printemps une déviation, etc."

And this view, that fungi already well known to mycologists were called forth by the punctures of insects, was regarded as not out of harmony with the idea that the fungus itself was an abnormal outgrowth of the tissues of the host.

The proper study of plant pathology presupposes and involves a knowledge of the physiology of plants, of the normal relations of the latter to their environment, and of the biology of those animals and plants (principally insects and fungi) which are parasitic on them. It is of the first importance to understand that a disease is a condition of abnormal physiology, and that the boundary lines between health and ill-health are vague and difficult to define. As with the study of the diseases of man and other animals, so with those of plants, the practice resolves itself into the accurate observation and interpretation of symptoms (*Diagnosis*) on the one hand, and of causes (*Aetiology*) on the other, before any conclusions of value can be drawn as to preventive or remedial measures (*Therapeutics*). In plants, however, symptoms of disease are apt to exhibit themselves in a very general manner, or at any rate it may be that our perceptions of them differentiate symptoms due to very different reactions imperfectly, probably because the organisation of the plant is less specialised than that of animals. The turning yellow and premature falling of leaves, for instance, is a frequent symptom of disease; but it may be due to a long series of different causes of ill-health—*e.g.* drought, too high or too low a temperature, light of insufficient or of excessive intensity, a superfluity of water at the roots, the presence in the tissues of parasitic fungi, or that of worms or insects at the roots or elsewhere, poisonous gases in the air, soil, etc., and so

forth. Consequently the science of plant pathology is much concerned with the direct action of external causes, which are probably less obscure than in the case of animals, though by no means always obvious. Such considerations at any rate seem to account for the fact that most authorities on plant pathology base their classification on the causes of disease, there being few noteworthy exceptions.

Notes to Chapter IX.

The bibliography here quoted will be found in Berkeley, "Vegetable Pathology," *Gardener's Chronicle*, 1854, p. 4; Plowright, *British Uredineæ and Ustilagineæ*, 1889; Eriksson and Henning, *Die Getreideroste*, Stockholm, 1896; De Bary, *Comparative Morphology and Biology of the Fungi*, etc., 1887; Frank, *Die Krankheiten der Pflanzen*, 1895-96, and scattered in the works referred to in them and in the text.

CHAPTER X.

HEALTH AND DISEASE.

Variation—Disease—Comparison to a top. Health—Extinction of species—Natural demise. Examples of complex interactions in health—Interference, and tendencies to ill-health.

WHEN we come to enquire into the causes of disease, it appears at first an obvious and easy plan to subdivide them into groups of factors which interfere with the normal physiology of the plant. Scientific experience shows, however, that the easy and the obvious are here, as elsewhere in nature, only apparent, for disease, like health, is an extremely complex phenomenon, involving many reactions and interactions between the plant and its environment. If we agree that a living plant in a state of health is not a fixed and unaltering thing, but is ever varying and undergoing adaptive changes as its life works out its labyrinthine course through the vicissitudes of the also ever-varying environment, then we cannot

escape the conviction that a diseased plant, so long as it lives, is also varying in response to the environment. The principal difference between the two cases is, that whereas the normal healthy plant varies more or less regularly and rhythmically about a mean, the diseased one is tending to vary too suddenly or too far in some particular directions from the mean; the healthy plant may, for our present purposes, be roughly likened to a properly balanced top spinning regularly and well, whereas the diseased one is lurching here, or wobbling there, to the great danger of its stability. For we must recognise at the outset that disease is but variation in directions dangerous to the life of the plant. Health consists in variation also, but not in such dangerous grooves. That the passage from health to disease is gradual and ill-defined in many cases will readily be seen. In fact we cannot completely define disease. Mere abnormality of form, colour, size, etc., is not necessarily a sign of disease, in the usual sense of the word, otherwise the striking variations of our cultivated plants would suggest gloomy thoughts indeed, whereas we have reason to believe that many cultivated varieties are more healthy—in the sense of resisting dangerous exigencies of the environment—than the stocks they came from. Strictly speaking, no two buds on a fruit-tree are alike, and the shoots they produce vary in position, exposure, number, and vigour of leaves, and so forth. The minute variations here referred to are

not seen by the ordinary observer, but those who bud, graft and multiply by cuttings on a large scale know that such bud-variations are important, quite apart from more extensive "sports" which occasionally occur.

On the other hand, we have reason to believe that many species have died out gradually as the environment altered. These plants died because they did not vary sufficiently, or did not vary in the right directions; they became diseased with respect to the then prevailing conditions of normal physiology or health.

Disease, therefore, may be said to be variation of functions in directions, or to extents, which threaten the life of the plant, the normal in all cases being the state of the plant characteristic of the species.

Even now, however, we have not obtained a complete definition, because, since all plants die sooner or later, we have not excluded the natural demise of the individual or its parts, and no one would call the autumnal fall of leaves, or the withering of an annual after flowering, death from disease. Clearly then the idea of disease implies danger of premature death, and probably this is as near as we shall get to a satisfactory definition. Since this matter is of primary importance for our present theme, I will add the following instances for consideration.

A plant in perfect health and in the fullest exercise of all its functions, has its roots in a soil which is suitably warmed and aerated, contains

the right quantities of water which dissolve just the proper proportions of all the essential mineral salts, but nothing poisonous, while the soil itself has a texture such that the roots and root-hairs can extend and do their utmost in absorbing.

The leaves above are exposed to just the right intensity of light, in air which is not too dry, and is of suitable temperature and composition, containing no poisonous exhalations, etc.; and as the foliage is gently moved by the breeze, it manufactures carbohydrates at the optimum rate in the chlorophyll, and the so-called "elaborated sap" containing the dissolved organic food-supplies is prepared in the tissues in maximum quantities and of just the right degrees of concentration and quality for use in the buds, stem, roots, etc., for which it is destined as they draw on the supplies.

Between these assimilating organs, the leaves, and the absorbing roots, we have in the stem the wood, with its vessels adapted in quantity and calibre to convey the water containing dissolved salts from the absorbing roots to the leaves (to say nothing of other parts) and, separated from this wood by the cambium, we find the sieve-tubes and cortical tissues in suitable quantity conveying the "elaborated sap"—the solutions of organic food-materials from the leaves down to the roots, up to the buds, and elsewhere. Joining these cortical and wood tissues are adapted series of medullary rays which, apart from other connections, bring about the necessary interchanges of water and

"elaborated sap" with the cambium, the formative tissue which has to be fed and served by them, and which by its growth supplies new vessels and sieve-tubes, etc., to carry the continually increasing quantities of water and food substances as the roots and leaves increase in number and area, and thus enables this ideally correlated system to go on working at maximum energy.

Now suppose the same plant with its roots in an unsuitable soil—too dry or too poor in mineral supplies, for instance—the transpiring leaves above cannot obtain sufficient water and salts to supply their needs, but we will suppose hypothetically that they still assimilate under the same ideal conditions as before. The supplies now coming to the cambium are diminished, since the want of water and minerals compels the leaves to put aside any excess of carbohydrates (*e.g.* as stored starch-grains), and the plastic materials which do pass to the cambium so deficient in water cannot be directly utilised, and a starvation period sets in. Consequently the cambium forms less wood, and this will contain fewer and smaller vessels, and so reduce the conducting passages: fewer sieve-tubes also are constructed, and the paths of the water current and food supplies narrowed, which of course reacts on the tissues everywhere. The reserve substances may slowly be dissolved and distributed, however, and considerable quantities be passed in course of time into the roots, which, as opportunity offers, gradually employ them in making new roots, and if the disturbance has not gone too far and the

conditions do not become unfavourable, an increased root-supply may by its larger absorbing area gradually establish the former state of equilibrium of functions. But this at the expense of the plant, which is smaller, has fewer leaves and narrower water channels, etc., than a plant not thus checked, and it may take a long time to make up for the loss of time and stature thus incurred. Indeed if the plant is an annual no recovery at all may occur, the reserves passing into fruit and seeds instead of slowly supplying the roots as described.

If it be asked, can such a condition of affairs as that described really occur, we have only to think of a transplanted specimen with its roots maimed and put into unsuitable soil, or of plants in the open with feeding roots gnawed by an insect, etc., or of a tree hitherto in equilibrium with its fellows in a plantation suddenly set free by thinning and so forth.

Now take the case where the roots are maintaining their maximum functional activity, but the leaves—owing to want of light, too much moisture or too low a temperature of the air—are functionally depressed. Here we get a state of oversaturation with water set up, the tissues are turgid to bursting point, what supplies do traverse the sieve-tubes, cortex, etc., do so slowly and are excessively diluted, and the cambium again forms less wood, but the lumina of the vessels are larger and the lignification less complete. Growth in length is excessive, but more leaves are formed,

though they are apt to be abnormally thin and may be small. Little or no reserves are stored anywhere, and the watery tissues contain dangerously diffusible substances which may render them an easy prey to parasitic fungi. Here again, however, if the disturbance of equilibrium has not gone too far, and if the season permits, the new leaves may come into full activity and the situation be saved by transpiration and assimilation gradually increasing and restoring the equilibrium. But, as before, the plant has suffered, and shows the effect in its weak shoots, retarded flowering, and other ways.

Such plight as is here described may actually be attained in greenhouses where over-watering is the fault, and even in the open it is not uncommon in rainy summers, or in plantations where dominant trees get the upper hand and partially shade more slowly growing species, or in fields where rank grass is allowed to overwhelm crops of lower stature.

Now it will be evident that either of these typical cases of temporary disturbance of functional equilibrium may be carried too far: in the first case the plant may wilt and wither, in the second it may rupture and rot, to take these eventualities only. And yet it is difficult to call these indispositions diseases: they are rather examples of extreme departures from the normal standard of health, just on the borderland between health and disease. A step further, as it were, and disease supervenes: certain tissues die from want of water,

and a necrotic area is formed, or the cortex bursts and a wound is formed in another way, or some fungus gets a hold, and so on. These abnormal states are particularly apt to predispose the plant to disease—insects revel in such semi-wilted leaves and shoots crammed with reserves, and fungi in the water-logged leaves of the second case, while a cold dry wind is peculiarly fatal to such tissues.

Notes to Chapter X.

The reader may consult Hartig, *Diseases of Trees*, Eng. ed., 1894, Introduction ; Sorauer, *Pflanzen Krankheiten*, pp. 1-12, and Frank, *Die Krankheiten der Pflanzen*, B. 1, p. 5, for definitions of disease.

CHAPTER XI.

CAUSES OF DISEASE.

A. External causes—I. Non-living environment: soil, atmosphere, temperature—II. Living environment: plants, animals—Complex interactions—Predisposing causes—No one factor works alone—Tangled problems of natural selection involved. B. So-called internal causes.

It is customary to classify the causes of disease in plants into two principal groups—(1) those due to the action of the non-living environment —soil, atmosphere, physical conditions such as temperature, light, etc.; and (2) those brought about by the activities of living organisms—plants and animals of various species. Before passing to further subdivisions under these two heads, however, it is necessary to observe that no disease can be efficiently caused by an organism alone, since its powers for injury as a parasite, or otherwise, are affected by its non-living environment as well as by the host-plant. For instance, the

spores of a parasitic fungus which would infect and rapidly destroy a potato plant in moist warm weather may be showered on to such a plant with impunity if the air remains dry and cool—or on to a cabbage under any circumstances as far as we know.

Again, probably no one factor of the non-living environment ever suffices to induce a disease, possibly because no such thing as only one change at a time ever occurs. For instance, it is difficult to say, when a soil becomes sodden with water, whether the excess of water and dissolved matters, the want of air displaced by the water, the lowering of the temperature, or the accumulation of foul products, etc., is the principal factor in causing the damage which results, and we have to determine by the balance of experimental evidence which is the dominant factor in all such cases.

The study of aetiology of disease is in fact only a particular case of that of aetiology in general. Plants at high altitudes in the Alps acquire very different characteristics from the same species in the plains. Is this due to the low temperature, the rarer atmosphere, the more intense illumination, the changes in moisture, etc., etc.? The question is more difficult than it appears at first sight, and we must remember that, complex as are the factors working on the host, they are equally complex in their actions on a parasite attacking the host, whence the resulting disease becomes indeed a tangled problem of natural selection.

Finally it remains to say a few words about a numerous class of cases where no external cause of disease can be discovered. It was formerly the custom to group such cases of "Internal Causes" by themselves, but apart from the fact that many of these mysterious diseases have subsequently been shown to be due to the action of external agencies, the whole question of internal causes resolves itself into one of relations between the plant and its surroundings, and it becomes evident that no inherited or internal disease can be regarded as explained until we know the external causes which have so modified the structure and working of the living cells as to make them abnormal in their reactions to other parts of the plant. "Internal causes" of disease, therefore, is a phrase expressing our ignorance, but somewhat more emphatically than usual. If this is clearly understood there seems no reason against its employment for the time being in the artificial scheme of classification we require. With regard to external causes due to the non-living environment, excess or deficiency of materials in the soil, water, or atmosphere plays an important part, and—since we may neglect purely aquatic plants—it is customary to speak of diseases due to unsuitable soils or to injurious atmospheric influences. For instance, any deficiency in the supplies of the necessary mineral salts (compounds of calcium, magnesium, potassium with sulphuric, nitric and phosphoric acids, etc.) leads to pathological changes, as also does the lack of the necessary traces of iron. But it is equally

true that the presence of such ingredients in excess or in combinations unsuited to the plants also leads to disaster, as also does the presence of minerals or other compounds which poison the root-hairs—*e.g.* products of decomposition, soluble salts of copper and other poisons. That these matters are bound up with the whole question of manuring and of proper soil-analyses will be evident.

Another essential factor is the nature and quantity of organic materials in the soil, whether leaf-mould and decomposing vegetable remains, stable manures, or other animal matters, all of which affect different species very differently, and produce very different results in different soils. It is necessary to apprehend in this connection what has been stated above: that soil is not a mere dead structureless medium, and that the root-hairs of ordinary plants cannot deal with large quantities of putrefying organic matter: that a good soil must abound in useful bacteria and fungi to render such substances available—and in very various ways—and that it must be open and aerated, of proper temperature and suitably supplied with water, and so forth, or disaster will result. Here, again, then we are brought into close contact with all that is known of fermentation, nitrification, and the various biological changes going on in soil, and the application of such knowledge to the practice of manuring and tillage in all its forms.

In view of the above remarks, the danger of "over-feeding," in this sense, has a real meaning

for horticulturists, though it must not be forgotten that no substance is really a food until it is assimilable into the protoplasm: manures, etc., are food-materials, not food. The futility of mere chemical analyses to prove what a plant requires is now well known, and it is only on the basis of long and carefully conducted experiments that we can ever discover what a particular plant in a particular soil, situation, and climate requires for healthy development. Again, the quantity of water in soil may be too great or too small for given species, and this either on the average for the year, or during critical periods only; and it is obviously important whether the excess or deficiency is due to improper supplies of water, the depth or shallowness of the soil, its retentive powers, or the nature of the sub-soil and so on, again bringing the whole matter into connection with our understanding of the physical constitution and structure of soils, and the nature of soil-drainage.

For instance, a common way of killing ferns is to keep the roots and soil wet and the air and fronds dry, whereas the natural habitats provide for wet and shaded fronds and well-drained soil.

It may be noted here that in most cases where gardeners speak of plants being killed under the "drip" of trees—*e.g.* Beech, the injury is due, not to the effects of water but to the shade: the loss of light is so great that the shaded plants die of inanition because their leaves are not able to provide sufficient carbohydrates.

Closely bound up with this is the question of the gases in soils. Apart from the disastrous effects of poisons—*e.g.* coal gas escaping from pipes under pavements in towns, etc., diseased conditions often result from deficiency of oxygen at the root-hairs, due to imperfect aeration of soils, brought about by stagnant water, excess of animal matter, and so forth.

Unsuitable constitution of the atmosphere is also a fruitful source of disease, though its effects are commoner in closed stoves and greenhouses than in the open. Nevertheless the continual exhalation of sulphurous fumes, chlorine, and other poisonous gases in the neighbourhood of manufacturing centres or of large smoky towns, volcanoes, etc., play their part in injuring plants; and excessive moisture in the form of mist, rain, etc., is also important. All these matters bring us at once into the region of physiology, and only an intelligent appreciation of what is known about the action of the atmosphere on the soil and the plant will save the peasantry of a country from a hopeless mysticism but little removed from that of the Middle Ages, when blights and other evils were vaguely referred to the river-mists, thunder clouds, and easterly winds.

If we summarise the above as the material factors of the environment, we may classify another set of external non-living causes of disease as the non-material factors. Such are principally the following:

The space at the disposal of plants greatly

affects their welfare. The crowding of roots in the soil and of foliage in the air, resulting in the loss of light to the leaves, involves deficiency of all the materials referred to above—minerals, organic materials, gases, and water—and no better illustration of the intense struggle for existence among these apparently passive and motionless beings, plants, can be given than an over-crowded seed-bed or plantation. If left to themselves such over-stocked areas exhibit to the keen eye of the trained observer all the phases of starvation, weakness, wounding, rot, and, so to speak, brutal dominance of the stronger over the weaker which it is the object of cultivation to prevent. Here, then, we are brought face to face with the true significance of thinning and weeding out, pruning, and similar processes.

Unsuitable temperature is one of the commonest of all sources of disease, for every plant is adapted to certain ranges of temperature, and best adapted to a given optimum somewhere between the maximum and minimum temperature for each function. Consequently any serious departure from the mean may bring about physiological disturbances of the nature of disease, and this in very various ways, as exemplified by the results of frost, sun-scorching, drought, hail-storms, forest fires, and so forth.

As a predisposing factor to disease abnormal temperature effects play a great part. Many wound-fungi gain their entrance through frost-cracks, bruises due to hailstones, or into tissues chilled below the normal.

No less remarkable are the diseases primarily due to insufficient or improper exposure to light, which affects the chlorophyll-apparatus and the process of carbon-assimilation and through these the whole well-being of the plant. Every plant is adapted to certain ranges of light intensity, and most cultivators know how impossible it is to grow shade plants in fully exposed situations, and how easily plants which live in open sunny situations are "drawn" and killed by shade. It is equally important to have the right kind of light, as disastrous experiences with greenhouses glazed with glass which cut off certain rays of light have taught. Here, again, it is important to notice that the optimum intensity or quality of light may differ for different functions and organs of the plant, as is shown by many adaptations on the part of species growing in natural situations—*e.g.* bud protection, orientation of leaves, etc.—and it may be taken as a rule that etiolated plants are peculiarly susceptible to other diseases.

As regards other factors of the inorganic environment, disasters which come within the scope of our subject may be brought about by many agencies, the mechanical effects of snow and hail, wind, avalanches, etc., the effects of lightning, and so forth, being a few of them.

Notes to Chapter XI.

For other detailed classifications of the causes of disease the reader is referred to the works of Sorauer and of Frank

referred to in the last chapter. Also Kirchner, *Pflanzen Krankheiten*, Stuttgart, 1890.

Of more historical importance are the older classifications of Berkeley, *Gardeners' Chronicle*, 1854, and Re, *Gardeners' Chronicle*, 1849-50. These latter are interesting as showing the very different views held by the earlier workers, and comparison of these with the modern views helps to mark the progress of physiology during the half century which has intervened.

CHAPTER XII.

CAUSES OF DISEASE. THE LIVING ENVIRONMENT.

Causes due to animals — Vertebrata — Wounds, etc. — Invertebrata —Insects, etc.—Plants as causes of disease—Phanerogams, weeds, etc. —Cryptogams, fungi —Epidemics, etc.

PASSING now to those causes of disease which are connected with the living environment, we may obviously divide them into two groups of agents, animals and plants.

Among animals, the various vertebrata, including man, are especially responsible for the larger kinds of wounds and wholesale destructive processes due to breakage, stripping of leaves and bark, cutting and biting, and so forth. Cattle, rabbits, rats and mice, squirrels and birds of various kinds stand out prominently as enemies to trees and other plants, to which they do immense injury in various ways by their horns, teeth, claws, and beaks; and the damage which an ignorant

gardener or forester can do with his ill-guided footsteps, axe, spade, and knife can only be appreciated by one who knows the habits of plants.

It is among the invertebrata, however, especially insects and worms, that the most striking agents of disease in plants are to be found, for, with the exception of certain rodents—and we may logically include also human invasions—vertebrate animals do not often appear in such numbers as to bring about the epidemics and scourges only too commonly caused by insect pests.

Insects injure plants in very various ways. Some, such as locusts, simply devour all before them ; others, *e.g.* caterpillars, destroy the leaves and bring about all the phenomena of defoliation. Others, again, eat the buds—*e.g. Grapholitha* ; or the roots—*e.g.* wire-worms, and so maim the plant that its foliage and assimilation suffer, or its roots become too scanty to supply the transpiration current. Many aphides, etc., puncture the leaves, suck out the sap, and produce deformations and arrest of leaf-surface, as well as actual loss of substance, and when numerous such insects induce all the evils of defoliation. Others, such as the leaf-miners, tunnel into the leaves, with similar results on a smaller scale.

It must be remembered that a single complete defoliation of a herbaceous annual, or even of a tuberous plant like the potato, so incapacitates the assimilatory machinery of the plant, that no stores can be put aside for the seeds, tubers, etc., of

another year, or at most so little that only feeble plants come up.

In the case of a tree the case is different, and since most large trees in full foliage have far more assimilatory surface than is actually necessary for immediate needs, a considerable tax can be paid to parasites or predatory insects before the stores suffer perceptibly. Still, it should be recognised that the injury tells in time, especially in seed years.

Many larvae of beetles, moths, etc., bore into the bark and as far as the cambium or even into the wood or pith of trees, the local damage inducing general injuries in proportion to the number of insects at work: moreover, the wounds afford points of entrance for fungi and other pests.

Galls and similar excrescences result from the hypertrophy of young living tissues pierced by the ovipositors of various insects, and irritated by the injected fluid and the presence of the eggs and larvae left behind. They may occur on the buds, leaves, stems, or roots, as shown by various species of *Cynips* on oak, *Phylloxera* on vines, etc., in all cases the local damage being relatively small, but the general injury to assimilatory, absorptive, and other functions is great in proportion to the number of points attacked.

Many grubs—larvae of flies, beetles, etc.—bore into the sheaths or internodes of grasses, or the pith of twigs, or into buds, fruits, and other organs of plants, and do harm corresponding to the kind and amount of tissues injured.

Various species of so-called eelworms—Nematodes—also cause gall-like swellings on young roots, or they invade the grains of cereals.

Finally, various slugs and snails cause much injury by devouring young leaves and buds and diminishing the assimilatory area.

Plants as agents of disease or injury fall naturally into the two main categories of flowering plants (Phanerogams) and Cryptogams, among which the fungi are the especially important pests.

Beginning with weeds, we find a large class of injurious agents. Weeds damage the plants we value by crowding them out in the struggle for existence, as already stated, and when the weed-action is simply due to superfluous plants of the same species, we speak of overcrowding. But it must not be overlooked that the competition between crowded plants of the same species—where every individual is acting as a weed to the others—may be more dangerous than between plants and weeds belonging to other species and genera, because in the former case they are struggling for the same minerals and other necessary food-materials: a matter of importance in connection with the rotation of crops.

The question of allowing grass to grow at the foot of fruit trees, as in orchards, is a good case in point. Such grass may increase the damp and shade, thus favouring fungi at one season, and dry up the moisture of the soil to the injury of the fine superficial roots at another, as well as exhaust the soil, owing to the competition of the

roots for salts and other materials. On the other hand, the checking of surface roots by competition with the grass has been claimed as advantageous. In this connection probably the whole question of the composition of the turf arises, as well as that of possible cropping for hay, and manuring.

As regards any particular weed, the cultivator should learn all he can respecting its duration, seeding capacity, method of dissemination, the depth and spread of its root-system, and any other particulars which enable him to judge when and how to attack it. It is only necessary to see the victory of such drought-resisting weeds as *Hieracium pilosella*, Plantains, *Hypochaeris*, on lawns to realise how weeds may win in the struggle for existence with the finer grasses.

Many so-called weeds are, however, partially parasitic, with their roots on the roots of others—*e.g. Rhinanthus*, *Thesium*, etc., and much damage is done to meadow grasses and herbage by the exhaustive tax which these semi-parasites impose.

This is carried still further in the case of such root-parasites as *Orobanche*, where the host-plant is burdened with the whole support of the pest, because the latter, having no chlorophyll, is entirely dependent on the former for all its food.

Even ordinary climbing plants may injure others by shading them, either by scrambling over their branches—*e.g.* Bramble, or twisting their tendrils round the twigs—*e.g.* Bryony, or twining round them—*e.g.* Woodbine, *Convolvulus*, etc. The principal direct injury is in these cases owing to

the loss of light suffered by the shaded foliage, but the weed-action is often increased by the competition of their roots—*e.g.* briars; and in the case of woody climbers the gradually increased pressure of the woody-coils round the thickening stems compresses the cambium and cortex of the support and induces strictures and abnormalities which may be fatal in course of time.

Epiphytes, or plants which support themselves wholly on the trunks, branches, or leaves of other plants, also injure the latter more especially by shading their foliage—*e.g.* tropical Figs, Orchids, Aroids, etc.; and similar damage is done by our own Ivy, the main roots of which are in the soil, but the numerous adventitious roots of which cling to the bark.

When the climber or epiphyte is also parasitic, as in the case of the Dodder, *Loranthus*, Mistletoe, etc., the direct loss of substance stolen from the host by the parasite comes in to supplement any effect of shading that the latter may bring about if it is a leafy plant.

Of Cryptogams, apart from a few epiphytic ferns, and the intense weed-action of certain Equisetums, the rhizomes and roots of which are as troublesome as those of twitch and other phanerogamic weeds, it is especially the fungi which act as agents of disease, and which, as we now know, are *par excellence* the causes of epidemics.

The action of fungi may be local or general; and restricted, slow and insidious, or virulent and rapidly destructive.

Examples of local action are furnished by *Schinzia*, which forms gall-like swellings on the roots of rushes; *Gymnosporangium*, which induces excrescences on the stems of junipers, and numerous leaf-fungi (*Puccinia*, *Æcidium*, *Septoria*, etc.), which cause yellow, brown, or black spots on leaves, as well as by *Ustilago*, which attacks the anthers or the ovary of various plants, and so forth. In such cases the injury done by a few centres of infection is very slight, but prolonged action may bring into play secondary effects such as the gradual destruction of the cambium round a branch, when, of course, the effect of ringing results; or if the fungus becomes epidemic and myriads of leaf-spots are formed, the destruction of foliar tissue, gradual taxing of the assimilatory cells, etc., may end in rapid defoliation, and renewed attacks soon exhaust the plants and lead to sterility and death, as often occurs with Uredineae—*e.g.* the coffee leaf-disease.

It is highly probable that such fungi are particularly exacting owing to their exhausting demands for compounds of potassium, phosphoric acid, and other bodies.

Examples of virulent and rampant general action are afforded by finger and toe in turnips, etc., where the roots are invaded by *Plasmodiophora*, which induces hypertrophy and rotting of the roots; and by the damping off of seedlings, where the fungus *Pythium* rapidly invades all parts of the seedlings and reduces them to a water-logged, putrefying mass; or the potato-disease, which is due

to the rapid spread of *Phytophthora* in the leaves and throughout the plant, which it blackens and rots in a few days.

Many fungi not in themselves very virulent or aggressive do enormous harm owing to the secondary effects they induce. Some of the tree-killing hymenomycetes, such as *Agaricus melleus*, for instance, penetrate the wood of a pine at the collar, and the result of the large flow of resin which results is to so block up the water passages that the tree dies off above with all the symptoms of drought. Similarly, the *Peziza* causing the larch disease, having obtained access to the stem about a foot or so above the ground, will gradually kill the cambium further and further round the stem, and so girdle the tree as effectually as if we had cut out the new wood all round. In all such cases—and the same applies to the leaf-diseases referred to above—the fungus may be compared to an army which is not strong enough to invade the whole territory, but which, by striking at the lines of communication, cuts off the supplies of water, food, etc., and so brings the struggle to an end. Indeed we might compare the cases of fungi which attack the root and collar, and so strike at and cut off the water supply, to a compact army which at once cuts off the enemy from his narrow base; whereas the innumerable units which bring about an epidemic attack on the leaves, and so surround the enemy and cut off his food supplies all round, is rather like a much larger army which cannot get in

beyond the natural barriers of the tissues, and so puts a *cordon* all round the territory and seizes the multitudes of food-stuffs at the frontiers. The end result is similar in both cases, but the methods of warfare differ.

Many fungi, however, though they make their presence noticeable by conspicuous signs, cannot be said to do much damage to the individual plant attacked. The extraordinary malformations induced by parasites like *Exoascus*, which live in the ends of twigs of trees and stimulate the buds to put out dense tufts of shoots, again densely branched—Witches' brooms—are a case in point. Also the curious distortions of nettle stems swollen and curved by *Æcidium*, of maize stems and leaves attacked by *Ustilago*, and of the inflorescences of *Capsella* by *Cystopus*, etc., are not individually very destructive; it is the cumulative effects of numerous attacks, or of large epidemics, which tell in the end.

Some very curious effects are due to fungi such as *Æcidium elatinum*, which, living in the cortex of firs, stimulate buds to put out shoots with erect habit, and with leaves which are radially disposed, annually cast, and differently shaped from the normal—characters quite foreign to the species of fir in its natural condition.

Equally strange are the shoots of *Euphorbia* infested with the æcidia of *Uromyces*, those of bilberries affected with *Calyptospora*, etc. In all these cases we must assume a condition of toleration, so to speak, on the part of the host, which adapts itself to the altered circumstances by marked

adaptations in its tissue developments, mode of growth and so forth.

This toleration is perhaps most marked in the case of those cereals which, though infected by the minute mycelium of *Ustilago* while still a seedling, nevertheless go on growing as apparently healthy green plants indistinguishable from the rest, although the fine hyphae of the parasite are in the tissues and keeping pace with the growth of the shoots just behind the growing points. As the grains of the cereal begin to form and swell, however, the hyphae suddenly assume the part of a dominant aggressor, consume the endosperm of the enlarging seed, and replace the contents of the grain with the well-known black spores known as Smut.

Notes to Chapter XII.

The reader will find a summary of such fungi as are here concerned in Massee, *A Text-Book of Plant Diseases*, 1899, or Prilleux, *Maladies des Plantes Agricoles*.

For further details the student should consult the works of Frank and Sorauer referred to in the notes to Chapter IX., and Tubeuf, *The Diseases of Plants*, Engl. ed. 1897, pp. 104-539.

For experiments on the effects of grass on orchard trees, see *Report of the Woburn Experimental Fruit Farm*, 1900, p. 160.

For the further study of weeds, the interesting bulletins of the Kansas State Agricultural College, 1895-1898, will show the reader what may be done in the matter of classifying them according to their biological peculiarities.

In regard to insects, the reader will find the following list embraces the subject: Somerville, *Farm and Garden Insects*,

1897 ; Theobald, *Insect Life*, 1896 ; Ormerod, *Manual of Injurious Insects*, 1890, and *Handbook of Insects Injurious to Orchards, etc.*, 1898.

The admirable series of publications of the U.S. Department of Agriculture under the editorship of Riley and Howard, and entitled *Insect Life*, 1888-1895, also abounds in information.

Further, Taschenberg's *Praktische Insektenkunde*, 1879-1880, and Judeich and Nietsche, *Lehrbuch der Mitteleurop. Forst. Insektenkunde*, 1889.

For an elementary introduction to the study of fungus diseases, see Marshall Ward, *Diseases of Plants*, Soc. for Promoting Christian Knowledge, London.

CHAPTER XIII.

NATURE OF DISEASE.

General and local disease—General death owing to cutting-off supplies, etc.—Disease of organs—Tissue-diseases, e.g. timber—Root-diseases—Leaf-diseases, etc.—Diseases of Respiratory, Assimilatory, and other organs—Physiological and Parasitic diseases—Pathology of the cell—Cuts—Cork—Callus—Irritation—Stimulation by protoplasm—Hypertrophy.

On going more deeply into the nature of those changes in plants which we term pathological or diseased, it seems evident that we must at the outset distinguish between various cases. A plant may be diseased as a whole because all or practically all its tissues are in a morbid or pathological condition, such as occurs when some fungus invades all the parts or organs—*e.g.* seedlings when completely infested by *Pythium*, or a unicellular Alga when invaded by a minute parasite; or it may die throughout, because some organ with functions essential to its life is

seriously affected—*e.g.* the roots are rotten and cannot absorb water with dissolved minerals and pass it up to the shoot, or all the leaves are infested with a parasite and cannot supply the rest of the plant with organic food materials, in consequence of which parts not directly affected by any malady become starved, dried-up, or poisoned or otherwise injured by the results or products of disease elsewhere.

In a large number of cases, however, the disease is purely local, and never extends into the rest of the organs or tissues—*e.g.* when an insect pierces a leaf at some minute point with its proboscis or its ovipositor, killing a few cells and irritating those around so that they grow and divide more rapidly than the rest of the leaf tissues and produce a swollen hump of tissue, or gall; or when a knife-cut wounds the cambium, which forthwith begins to cover up the dead cells with a similarly rapid growth of cells, the callus. Numerous minute spots due to fungi on leaves, cortex, etc., are further cases in point, the mycelium never extending far from the centre of infection.

Many attempts have been made to classify diseases on a basis which assumes the essential distinction of the above cases, and we read of diseases of the various organs—root-diseases, stem-diseases, leaf-diseases, and so forth; or of the various tissues—timber-diseases, diseases of the cambium, of the bark, of the parenchyma, and so on. Furthermore, attempts have been made to speak of general functional disease, of

diseases of the respiratory organs, of the absorptive organs, and so forth, as opposed to local lesions.

Critical examination, however, shows that no such distinctions can be consistently maintained, partly because the organs and functions of plants are not so sharply marked off as they are in animals, the diseases of which have suggested the above classification, and partly because all disease originates in the cells and tissues, and it is a matter of detail only that in some cases—*e.g.* severe freezing or drought of seedlings, or when some ingredient is wanting in the soil—the diseased condition affects practically every cell alike from the first, while in others it spreads more or less rapidly from some one spot.

Even the distinction into physiological diseases *versus* parasitic diseases cannot be maintained from the standpoint of the nature of the disease itself. All disease is physiological in so far as it consists in disturbance of normal physiological function, for pathology is merely abnormal physiology, no matter how it is brought about. This is not saying that no importance is to be attached to the mode in which disease is incurred or induced: it is merely insisting on the truth that the disease itself consists in the living cell-substance—the protoplasm—not working normally as it does in health, and this, whether want of water, minerals, or organic food be the cause, or whether the presence of some poison or mechanical irritant be the disturbing agent, as also whether

such want or irritation be due to some defect in soil or air, or to the ravages of a fungus or an insect.

This being understood I need not dwell on the common fallacy of confounding the fungus, insect, soil or other agent with the disease itself, or of making the same blunder in confusing symptoms with maladies. In this sense, wheat rust is not a disease : it is a symptom which betrays the presence of a disease-inducing fungus, the Rust fungus. Similarly, chlorosis is not a disease : it is a symptom of imperfect chlorophyll action, and the best proof of the truth of both statements is that in both cases the fundamental disease-action is the starvation of the cell-protoplasm of carbohydrates and other essential food matters—in the one case because the fungus steals the carbohydrates as fast as the leaves can make them, in the second because the leaf is unable to make them.

The foundation of a knowledge of disease in plants therefore centres in the understanding of the pathology of living cells.

If a suitable mass of living cells is neatly cut with a sharp razor the first perceptible change is one of colour : the white "flesh" of a potato or an apple, for instance, turns brown as the air enters the cut cells, and the microscope shows that this browning affects cell-walls and contents alike. The cut cells also die forthwith ; and the oxygen of the air combining with some of their constituents forms the brown colouring matter which soaks into the cell-walls. The uninjured cells below them

grow longer, pushing up the dead débris, and divide across by walls parallel to the plane of the wound, and so form series of tabular cells with thin walls, which also soon turn brown and die, the cell-walls meanwhile undergoing changes which convert them into cork. The living cells deeper down are now shut off from the outer world by a skin, of several layers, of cork-cells, which prevent the further free access of air or moisture. During the period of active cell-division which initiates the cork, the temperature of the growing cells rises: a sort of fever (wound-fever) is induced, evidently owing to the active respiration of the growing cells.

This healing by cork occurs in any tissue of living cells exposed by a cut—leaf-tissue, young stem or root, fruit, cambium, etc.; and the same applies to any other kind of cutting or tearing injury—such as a prick with a needle or the proboscis of an insect, a stripping, or even a bruise.

Such healing is prepared for and carried out very thoroughly in the case of falling leaves and cast branches, the plane of separation being covered by a cicatrix of cork.

If the cell-tissue under the wound is actually growing at the time, however, a further process is observed when the wound-cork has been formed. The uninjured cells below go on growing outwards more vigorously than ever, the pressure of the overlying tissues taken off by the cut having been removed, and, lifting up the cork-layer as they do so, they rapidly

divide into a juicy mass of thin-walled cells which is of a cushion-like nature and is termed a *Callus*. This callus is at first a homogeneous tissue of cells which are all alike capable of growing and dividing, but in course of time it undergoes changes in different parts which result in the formation of tracheids, vessels, fibres and other tissue-elements, and even organs, just as the embryonic tissues of the growing points, cambium, etc., of the healthy plant give origin to new growths. Such wound-wood, however, is apt to differ considerably in the arrangement, constitution and hardness of its parts as compared with normal wood, and its peculiar density and cross-graining are often conspicuous.

If instead of a simple tissue, the cut or other wound lays bare a complex mass such as wood, the resultant changes are essentially the same to start with. The living cells bordering the wound form cork, and then those deeper down grow out and form a callus. The exposure of the wood however, entails alterations in its non-living elements also. The lignified walls of tracheids, fibres, etc., turn brown to a considerable depth, and this browning seems to be—like all such discolorations in wounds—due to oxidation changes in the tannins and other bodies present: the process is probably similar to what occurs in humification and in the conversion of sap-wood into heart-wood in trees. Such wood is not merely dead, but it is also incapable of conveying water in the lumina of its elements, which

slowly fill with similarly dark-coloured, impervious masses of materials termed "wound-gum," the nature of which is obscure, but which slowly undergoes further changes into resin-like substances.

The exposure of wood by a wound results also in another mode of stopping up the vessels and so hindering the access of air, loss of water, etc., for the living cells of the medullary rays and wood-parenchyma grow into the lumina of the larger vessels through the pits, forming *thyloses*, again a phenomenon met with in heart-wood. In Conifers the stoppage of the lumina is increased by deposition of resin, which also soaks into the cell-walls and the wounded wood becomes semi-translucent owing to the infiltration.

Every living cell in an active condition is irritable, and one of the commonest physiological reactions of growing tissues is that of responding to the touch of a resistant body, as is vividly shown by the movements of the Sensitive plant, *Dionaea*, etc., and by those of tendrils, growing root tips, etc., on careful observation. We have reason for stating that if a minute insect, too feeble to pierce the cuticle, cling on to one side of the dome-shaped growing point of any shoot, the irritation of contact of its claws, hairs, etc., would at once cause the protoplasm of the delicate cells to respond by some abnormal behaviour; and, as matter of experiment, Darwin showed long ago that if a minute piece of glass or other hard body is kept in contact with one side of the tip of a root, the growth on the side in contact is interfered

with. Moreover we know from experiments on heliotropism, thermotropism, etc., that even intangible stimuli such as rays of light, etc., impinging unsymmetrically on these delicate cells cause alterations in their behaviour—*e.g.* arrest or acceleration of growth.

Perhaps the most remarkable class of stimulations, however, is that due to the presence of the entire protoplasmic body of one organism in the cell of another, each living its own life for the time being, but the protoplasm of the host cell showing clearly, by its abnormal behaviour, that the presence of the foreign protoplasm is affecting its physiology. A simple example is afforded by Zopfs' *Pleotrachelus*, the amoeboid protoplasmic body of which lives in the hypha of *Pilobolus*, causing it to swell up like an inflated bladder, in which the parasite then forms its sporangia. The *Pleotrachelus* does not kill the *Pilobolus*, but that its protoplasm alters the metabolic physiology of the latter is shown by the hypertrophy of the cells, and by the curious fact that it stimulates the *Pilobolus* to form its sexual conjugating cells, otherwise rare, an indication of very far-reaching interference with the life-actions of the host.

An equally remarkable example is that of *Plasmodiophora*, the amoeboid naked protoplasm of which lives and creeps about in the protoplasm of a cell of the root of a turnip, to which it gains access through the root-hairs. It does not kill the cell, but stimulates its protoplasm to increased activity and growth and division, itself dividing also

and passing new amoebae into each new daughter-cell of the host. Here the processes of stimulation, hypertrophy and further division are repeated, until hundreds or thousands of the turnip root-cells are infected. The externally visible result is the formation of distorted swellings on the root (Finger and Toe), most of the cells of which are abnormally large and filled with amoeboid *Plasmodiophora* protoplasm, which finally devours the turnip-protoplasm and itself passes over into spores. Here we have most convincing proof of the stimulation of protoplasm by other protoplasm in direct contact with it; and that the metabolism of the host-cells is profoundly altered is shown not only by the abnormal growth of the cells, but also by the starvation of the rest of the turnip plant as the *Plasmodiophora* gets the upper hand. We have here, in fact, a local intracellular parasitic disease, gradually invading large tracts of tissue and eventually inducing general disease resulting in death—a state of affairs reminding us of cancer in animals.

Irritation and hypertrophy of cells, however, may be induced by parasites which never bring their protoplasm into direct contact with that of the host. Many Chytridiaceae penetrate the cells of plants, and grow inside them as short tubes, vesicles, etc., the protoplasm of which is separated by their own cell-walls from that of the host-cell; nevertheless hypertrophy and abnormal cell-divisions and secretions are induced, and the effect even extends to neighbouring cells—*e.g.* *Synchytrium*—showing

that some influence is exerted through cells themselves not directly affected. This latter point need not surprise us now we know that the cells of plant-tissues are connected by fine protoplasmic strands passing through the separating cell-walls.

But the invading plant need not actually enter the cells, and may still stimulate them through both its own and their own cell-walls to abnormal growth. This is well shown by the intercellular mycelium of *Exoacus* and *Exobasidium*, and the latter affords an excellent illustration of the far-reaching effects of hyphae on the cells (of *Vaccinium*) into which they do not penetrate. Not only are the cells stimulated to grow larger and divide oftener than normally, thus producing large gall-like swellings, but the chlorophyll disappears, the cell sap changes colour to red, the numerous compound crystals normally found in the tissues diminish in number and are different in shape, large quantities of starch are stored up, and even the vascular bundles are altered in character. All these changes indicate very profound alterations in the physiological working of the protoplasm of the cells of the host, and yet the fungus has done its work through both its own cell-walls and those of the host.

Even harmless endophytic algae in the intercellular spaces of plants may stimulate the cells in their immediate neighbourhood to increased growth, *e.g. Anabaena* in the roots of Cycads.

Notes to Chapter XIII.

With reference to cork-healing and wound-fever the student may consult Shattock "On the Reparative processes which occur in Vegetable Tissues," *Journal of the Linnean Society*, 1882, Vol. XIX., p. 1; and Shattock "On the Fall of Branchlets in the Aspen," *Journal of Botany*, 1883, Vol. XXI., p. 306. Also Richards, "The Respiration of Wounded Plants," *Annals of Botany*, Vol. X., 1896, p. 531; and "The Evolution of Heat by Wounded Plants," *Ann. of Bot.*, Vol. XI., 1897, p. 29.

For details and figures respecting callus, see Sorauer, *Physiol. of Plants*, p. 175.

In respect to the irritable movements referred to see Darwin, *The Power of Movements in Plants*, 1880, chapter III. The recent work of Nawaschin, *Beobachtungen ueber den feineren Bau u. Umwandlungen von Plasmodiophora*, Flora, Vol. LXXXVI., 1899, p. 404, should be read for details and literature concerning "Finger and Toe."

CHAPTER XIV.

NATURE OF DISEASE (*Continued*).

Actions of poisons in small doses—Results of killing a few cells—Malformation—Enzymes—Secretions and excretions—Acids, poisons, etc.—Chemotactic phenomena—Parasitism—Epiphytes and endophytes—Symbiosis—Galls.

PHYSIOLOGICAL research has shown that the respiratory activity of cells may be increased by small doses of poisons, and even that growth may be accelerated by them—*e.g.* chloroform, ether—and, still more remarkable, that fermentative activity may be enhanced by minute doses of such powerful mineral poisons as mercuric chloride, iodine salts, etc., and that the cells may be gradually accustomed to larger doses without injury. Unfertilised eggs of insects have been started into growth by treatment with acids and those of frogs with mercury salts, and the germination of beans quickened by various poisonous alkaloids. In other words, graduated doses of

poison may alter the physiological activity of living cells, inducing pathological phenomena, while larger doses kill them.

Now we know at least one parasitic fungus which poisons the cells of its host, and kills them, with similar symptoms to those resulting from excessive doses of the above-named toxic agents. *Botrytis* hyphæ, living in the cell-walls of plants, but not entering the cells, excretes a poison which kills the protoplasm, and the fungus then feeds on the debris. Numerous other fungi form powerful poisons, but we do not know whether or how they employ them—*e.g.* Ergot.

It is obvious that if all the young cells of a root-tip or of the apex of a shoot, or those of a young leaf, are growing and dividing regularly, the killing of one or a few cells at one point on the side of the organ must result in irregularities—in malformation—of the adult organ. This has been proved experimentally by destroying a few cells with a needle. It can also be done by planting a minute mycelium of *Botrytis* laterally on a young organ—*e.g.* a very young lily-bud. The fungus adheres to the surface, kills a few epidermis cells, and forms a foxy-red spot, which becomes concave as the dead cells lose water and dry. Since the rest of the bud goes on growing, however, while this dead point remains stationary, the latter gradually becomes the centre of a concavity, the growing tissues having grown round it: the bud is deformed. Numerous cases of malformed organs are explained in this way; a minute insect has

bitten or pierced the young tissue, or a fungus has killed a minute area, or a drop of acid condensed from fumes in the air is the lethal agent, and so forth. And even on a much larger scale we see the same kinds of agents at work. Wherever a patch of cells is killed whilst those around go on growing, there must result some deformation of the resulting organ, since had the injury been withheld the number and sizes of the cells now fixed in death would have increased and covered a larger area: they now serve to pull over to their side the still living and growing cells. The same results follow on any lateral wound: the killed spot of tissue serves as a point round which the continued growth of other parts of the organ turns. Hence the malformation is in these cases a secondary effect, and not, as in simple hypertrophy, a direct effect of the action of the cells involved in the injury.

There is another class of bodies secreted by fungi, however, which act directly on cells, viz. enzymes—that is, soluble bodies which are able to dissolve cellulose *(cytases)*, starch *(diastases)*, proteids (proteolytic enzymes), and other substances, by peculiar alterations in their constitution. It is by means of its *cytase* that *Botrytis* hyphae pierce the cellulose walls of plants, and no doubt in all cases where fungi pierce cell-walls it is by the solvent action of such a cytase, and similarly when haustoria penetrate into the cells. It is also by means of these starch-dissolving enzymes (diastases) and proteolytic

enzymes, etc., that the hyphae inside the cells are enabled to make use of the starch, proteids, etc., they find there.

All living cells form materials, resulting from the activity of the protoplasm, which we may compare with the refuse or by-products formed in any great manufacturing industry: these by-products have to be got rid of if they are injurious or noisome *(excretions)*, and if not—*i.e.* if they are capable of further use *(secretions)*—they have to be stored away till required. Some of the most prominent of these bodies excreted by fungi are, as we have seen, poisonous acids, such as oxalic acid, enzymes, and organic poisons, such as those in ergot. But similar enzymes, acids, poisons, etc., to those found in fungi are also found in the cells of other plants and animals; for only by means of their solvent actions can processes like digestion and assimilation of the starchy and other materials into the body-substance be accomplished, and we have seen that it is a general property of living cells to form acids, and other excretions and secretions.

Now we know very little about what may happen when an organism—say a fungus—secreting especially one kind of enzyme or poison or other active substance, comes into intimate contact with another—say a leaf-cell—which secretes predominantly others, but what we do know points to the certainty that various complications will occur.

For instance, if certain bacteria which prefer an

alkaline medium, and yeasts which prefer an acid environment are mixed in a saccharine solution, it depends on the reaction of the liquid which organism gains the upper hand: if the liquid is acid the yeast may dominate the bacteria; if alkaline it may be suppressed by them.

That a parasite may be prevented from successfully attacking a particular plant is shown by the failure of *Cuscuta* to establish its haustoria in poisonous plants such as *Euphorbia*, *Aloe*, etc., and it has been pointed out that poisonous secretions in the cells of the plant protect them against the penetration of fungi. This cannot be taken as meaning that any poison protects against any parasite, however, for *Euphorbia* is itself subject to attacks of Uredinae, and *Pangium edule*, which contains prussic acid and is extremely poisonous to most animals, is eaten with avidity by several insects, while nematode worms can live in its tissues. This is no more remarkable, however, than the fact that *Fontaria*, a myriapod, secretes prussic acid in its own tissues, or than that certain glands of the stomach secrete free hydrochloric acid, and *Dolium* forms sulphuric acid in its glands.

There is yet a further point to notice here. It has been proved that certain substances formed in plant-cells, not necessarily nutritive, attract the hyphae of parasitic fungi or repel them, according to the kind and degree of concentration. So clear has this proof been made that it was possible in experiments conducted apart from a host plant,

to make the hyphae on one side of an artificial membrane—*e.g.* collodion—penetrate it by placing one of these attractive (*chemotropic*) substances in suitable proportions on the other side. The hyphae dissolved holes in the membrane by means of enzymes and plunged into the attractive substance on the other side.

The foregoing sketch gives us a glimpse into the causes at work in parasitism.

Suppose a fungus on the outside of the epidermis of a young organ—say a leaf. It may be unable to penetrate into the plant, and finding no suitable food outside it dies : or it may be satisfied with the traces of organic matter on the epidermis and then lives the life of a saprophyte. Or it may be able to establish a hold-fast on the tender epidermal surface, but without entering the cells, and irritate the developing organ by contact stimulation, inducing slight abnormalities ; if in its further, purely superficial growth such an epiphyte covers large areas of the leaf, and especially if the hyphae are dark coloured—*e.g. Dematium* and other "Sooty Moulds"—injury may be done to the leaf owing to the shading action which deprives the chlorophyll below of its full supply of solar energy. Some epiphytes, however, are able to fix their hyphae to the epidermis by sending minute peg-like projections into the cuticle—*Trichosphaeria, Herpotrichia*—while others send haustoria right through the outer epidermal walls—*e.g. Erysiphe*—and thus supplement mere contact-irritation and shading by

actual absorption from the external cells. Here the fungus is a parasitic epiphyte.

A stage further is attained in those fungi which enter the stomata and live in the intercellular spaces—*e.g.* many Uredineae and *Phytophthora*—and many such intercellular endophytes increase their attack on the cells by piercing their walls with minute (*Cystopus*) or large and branched (*Peronospora*) haustoria, or even eventually pierce the cells and traverse them bodily (*Pythium*). In all these cases it is clear that conflicts must occur between poison and antidote, acid and alkali, attractive and repellent substances, enzyme and enzyme, etc., as was hinted at above; and the same must take place when the parasite is endophytic and intracellular from the first, as in Chytridiaceae, etc., the zoospores of which pierce the outer cell-walls and forthwith grow into the cells. There are also fungi which, while able to pierce the outer cell-walls, and grow forward in the thickness of the wall itself, cannot enter the living cells themselves—*e.g.* *Botrytis*. In the example mentioned, the fungus excretes a poison, oxalic acid, which soaks into and kills the cells next its point of attack: into these dead cells it then extends, and, invigorated by feeding on them, extends into other cell-walls and excretes more poison, and so on.

On the basis of the foregoing it seems possible to sketch a general view of the nature of parasitism. In order that a fungus may enter the cells it must be able to overcome not only the resistance of the

cell-walls, but that of the living protoplasm also: if it cannot do the latter it must remain outside, as a mere epiphyte, or at most an intercellular endophyte. If it can do neither it must either content itself with a saprophytic existence or fail, so far as that particular host-plant is concerned. Its inability to enter may be due to there being no chemotropic attraction, or to its incapacity to dissolve the cell-walls, or to the existence in the cell of some antagonistic substance which neutralises its acid secretions, destroys its enzymes or poisons, or is even directly poisonous to it.

Moreover when once inside it does not follow that it can kill the cell. The protoplasm of the latter may have been unable to prevent the fungus enemy from breaking through its first line of defence—the cell-wall, but it may be quite capable of maintaining the fight at close quarters, and we see signs of the progress of the struggle in hypertrophy, accumulation of stores, and other changes in the invaded cells and their contents.

Finally, the invested or invaded cell may so adapt itself to the demands of the invader that a sort of arrangement is arrived at by which life in common—*Symbiosis*—is established, each organism doing something for the other and each taking something from the other. In this latter case, which is often realised—*e.g.* lichens, leguminous plants and the organisms in their root-nodules, mycorrhiza, etc.—we leave the domain of disease, which supervenes indeed if the other symbiont is lacking.

Some interesting facts bearing on the matters here under discussion, have been obtained from the study of *Galls*, the curious outgrowths found on many plants and due to the action of insects.

A typical gall exhibits three distinct and characteristic layers of tissue surrounding the hollow chamber in which the larva of the insect lies, viz., an outer layer of soft cells forming a parenchyma covered with an epidermis, and frequently also with a layer of cork; an inner stratum consisting of very thin-walled delicate cells filled with protoplasmic and reserve food-materials on which the larva feeds; and between the two a more or less definite layer of thick-walled sclerenchyma cells which serve as a protection against accidents to the larva as the outer layer shrivels or rots, or if it is exposed to the attack of marauders. This layer may be absent from galls which have a short life only. Vascular bundles run into the outer layer from the leaf-veins or the stele of the shoot, etc. Such galls abound in tannin, and are frequently of use in the arts on this account: they also contain starch, and proteid substances and crystals of calcium oxalate. When the larva has consumed the stores of food material and reached the adult stage it eats its way out and escapes.

The growth of such a gall is preceded by the laying of an egg on or in the embryonic tissue of a leaf, stem, or other young part, and it is interesting to note that only organs in the meristematic stage can form galls, and that it is

by no means necessary that the tissues should be wounded. Moreover, the egg as such is incapable of stimulating the plant tissues, but when it hatches, the resulting larva, beginning to feed on the cells, irritates the tissues and rapid growth and cell-division occur, as in the case of other wounds or of fungus attacks. The actual wound made by the ovipositor heals up at once. It is evident from numerous recent researches that these true galls are not due to any poisonous or irritating liquid injected by the parent, but that the stimulus to the tissue formation is similar to that exerted by a wound. The young gall is in fact a callus enclosing the living larva, and it is the continued irritation of the latter which keeps up the stimulation. The final shape and constitution of the gall depend on mutual reactions—not as yet explained in detail—between the species of plant and the species of gall-insect concerned, as may readily be seen from the extraordinary variations in size, shape, colouring, hairiness and other structural peculiarities of the galls on one species of, for instance, the common oak. From what we have learnt about fungus parasites, however, there can be little doubt that reactions between the cells and the larva of the insect occur, resembling those which take place between the cells and the hyphae of the fungus, and this is borne out by the study of other hypertrophies due to animals; *e.g.* Nematode worms in roots, and the remarkable galls—the simplest known—on *Vaucheria*, caused by the entrance into this alga of a species

of *Notommata*, which induces a different gall on each of the various species of its host plants.

It must be concluded that the formation of the *Vaucheria* gall is induced by the mechanical irritation which the Rotifer causes in the protoplasm. These galls are comparable to the hypertrophies in *Pilobolus* caused by the presence of *Pleotrachelus*.

Attempts to induce the development of galls artificially by injecting formic, acetic and other vegetable acids, poisons and other substances into the tissues have, however, failed, and even the substances contained in the insect or gall itself only produced negative results. Nothing further was obtained than slight callus formations in some cases. Nor have experimenters succeeded in obtaining more than slight distortions by fixing insects on the growing leaves in such positions that they could scratch the epidermis.

We must therefore conclude that very complex interactions between the plant and insect are here concerned, among which may be the infiltration of some liquid from larva to plant—many of these gall larvae are strongly scented, and Kustenmacher says that fluids excreted by the larva are absorbed by the gall-tissue apparently as nutriment. This would point to the symbiotic character of galls and their guests.

Notes to Chapter XIV.

With regard to the action of poisons in small doses see further Johannsen, *Das Aether-Verfahren beim Fruhtreiben*,

Jena, 1900, and, for *Botrytis*, see Marshall Ward, "A Lily Disease," *Annals of Botany*, Vol. II., 1889, p. 388.

The subject of enzymes has been exhaustively treated by Green, *The Soluble Ferments and Fermentations*, Cambridge, 1899, to which the reader is referred for literature. I have taken the statements regarding *Fontaria* and *Dolium* from Kassowitz, *Allgemeine Biologie*, p. 182. The two most important works on chemotactic phenomena are Pfeffer, "Uber Chemotaktische Bewegungen," etc., *Unters. aus dem Bot. Inst. zu Tubingen*, B. II., p. 582, and Miyoshi, "Die Durchbohrung von Membranen durch Pilzfäden," *Pringsh. Jahrb. f. Wiss. Bot.*, B. XXVIII., 1895, p. 269, and from these the further literature can be traced. As regards the nature of parasitism see Marshall Ward, "On Some Relations between Host and Parasite," etc., being the Croonian Lecture delivered before the Royal Society, *Proc. Roy. Soc.*, Vol. 47, p. 393. On Symbiosis, see Marshall Ward, "Symbiosis," *Annals of Botany*, 1899, Vol. XIII., p. 549, where the literature is collected. For a general account of galls the reader may consult Kerner, *The Natural History of Plants*, Eng. ed., 1895, Vol. II., pp. 527-554, and Adler, *Alternating Generations, A Biological Study of Oak Galls*, etc., 1894.

CHAPTER XV.

SPREADING OF DISEASE AND EPIDEMICS.

Dissemination of fungi by the aid of snails, rabbits, bees, and insects—Man—Distribution in soil, on clothes, through the post, etc.—Worms, wind—Puffing of spores—Creeping of mycelia—Lurking parasites—Spread of insects and other animals—Losses due to epidemics.

THE dissemination of plant diseases is a subject which has been far too much neglected, but our knowledge of it is slowly increasing. The spores of fungi such as Rusts and Erysipheae are often carrried from plant to plant by snails; those of root-destroying and tree-killing Polyporei by rabbits, rats, and other mammals which rub their fur against the hymenophores. Bees have been shown to carry the spores of *Sclerotinia* and infect the stigmas of Bilberries, etc., with them; and flies convey the conidia of Ergot from grain to grain. Insects, indeed, of all kinds are great disseminators of disease—as witness also the part played by

mosquitoes in transferring the malaria parasite to man—and beetles, bees, flies, etc., of all sorts probably play more active parts in this work than has yet been proved, since they not only carry spores attached like pollen to their hairy bodies, but in many cases in their alimentary canal, to be spread later in the dung.

The part played by man in conveying fungi from plant to plant counts for much. Not only do gardeners and farm labourers carry spores on their boots and clothes as they pass from infected to non-infected areas, but carted soil and manure are frequently infested with spores of Smuts, *Fusarium*, *Polyporus*, and the sclerotia or rhizomorphs of *Sclerotinia*, *Agaricus melleus*, *Dematophora*, etc. Man also sends diseases through the post, and by rail and ship, by spores or mycelia attached to seedlings, bulbs, fruits, flowers, etc., as shown in several cases of potato, vine, hollyhock, lily, and hyacinth diseases. Every time a carpenter saws a piece of fresh timber with the saw which has been used previously for cutting wood attacked with dry rot, he risks infecting it with the fungus. Similarly in pruning: every cut with a knife which the gardener has used on infected branches may infect the tree.

Cuttings made with a soil-contaminated knife and stuck into ordinary soil in dirty boxes covered with equally dirty glass, present every chance for infection by soil organisms; bacteria and fungi obtain access to the vessels, and derive plenty of food from the juices, and the wonder is not that

so many cuttings "damp off," but that any are raised at all under ordinary conditions.

That worms bring buried spores to the surface can hardly be doubted after Pasteur's experiments with Anthrax, and the principle of Darwin's discoveries of the important bearing of the habits of earthworms on this subject, and that the soil attached to the feet of ducks and other birds teems with small seeds, applies to fungi also. Wind is also responsible for distributing fungus-spores over wide areas, as may be easily proved by fixing a glass slide smeared with glycerine in the course of a breeze passing over an infected area.

But although the fungi are, generally speaking, passive in regard to their distribution, such is by no means always the case. Apart from the fact that some forms attract insects by means of honey dew (Ergot), or by sweet odours (Spermogonia, *Sclerotinia*), the zoospores of *Pythium*, *Phytophthora*, etc., are motile, and although they cannot move far in the films of water in which they travel, nevertheless in a wet potato field, with the wind flapping the leaves one against the other, some dissemination of importance must be actively brought about, and similarly with the amoebae of *Plasmodiophora* in the soil.

The shooting of ascospores into the air by certain species of *Peziza*, from the discs of which the spores may be seen to puff out in clouds, affords further evidence that fungi cannot be regarded as entirely passive in respect to distribution of their spores. But when we come to

certain of the soil fungi—*e.g. Agaricus melleus*, *Dematophora*, etc.—the active creeping forward by growth in the soil of their rhizomorphs and mycelial strands afford examples of active spreading of considerable importance in the vineyard and forest, since they pass from root to root and from tree to tree and may infect the entire area in course of time.

Not the least significant mode of dissemination is that by which what I have termed "lurking parasites" are spread: such are fungi which attach themselves to the seeds, fruits, tubers, etc., of other plants and so obtain all the advantages of being carried and sown with the latter—*e.g.* Ustilagineae and Uredineae which adhere to grain, *Verticillium*, *Nectria*, etc., in potatoes and other plants.

The spread of diseases due to animals, especially insects, is of course more active, in consequence of the motility of the distributing agents. This is most marked in the winged species, of which locusts, beetles, moths and butterflies, flies and wasps furnish well-known examples; and is not inconsiderable in the case of wingless and merely creeping species. It is noteworthy that many forms wingless in the parasitic stage are winged at certain periods, *e.g.* the females of *Phylloxera*.

That man also spreads insect pests is well known and acted upon, as witness the phylloxera laws—which, however, it is to be feared too often only illustrate once more the adage concerning the shutting of the stable door after the horse has gone.

It would be tedious to attempt anything like a complete account of the estimates of loss in different countries, due to the ravages of insects and fungi, but the following examples should surely serve to convince anyone of the magnitude of these losses and of the economic importance of the whole question, and the reader may be referred to the special literature for further details.

The coffee leaf-disease of Ceylon, due to the fungus *Hemileia*, is estimated to have cost that Colony considerably over £1,000,000 per annum for several years. One estimate puts the loss in ten years at from £12,000,000 to £15,000,000. The hop-aphis is estimated to have cost Kent £2,700,000 in the year 1882. In 1874 the Agricultural Commissioner of the United States estimated the annual loss, due to the ravages of insects on cotton alone, to amount to £5,000,000; and in 1882 the annual loss to the United States due to insects, calculated for all kinds of agricultural produce, was put at the appalling figure of from £40,000,000 to £60,000,000 sterling. In India, the annual loss due to wheat-rust alone has recently been estimated at 4,000,000 to 20,000,000 rupees, and one insect alone is said to have cost the cotton planters a quarter of the crop—valued at seven crores of rupees—in bad years. Similarly, in Australia the annual loss from wheat-rust has been put at from £2,000,000 to £3,000,000. In 1891 the loss in Prussia alone from grain-rusts was

officially estimated at over £20,000,000 sterling. Need more be said? Even allowing for considerable exaggerations in such estimates it is clear that the damage to crops in any country soon amounts to sums which even at low rates of interest would easily yield incomes capable of supporting the best equipped laboratories and staffs for investigations directed to the explanation of the phenomena in detail, the sole basis on which intelligent preventive and therapeutic measures can be based. But it is far from likely that the estimates are exaggerated. The planting and agricultural communities are as a rule opposed to the publication of statistics—or at least have been so in various countries and at different times—and if we knew the damage done to all crops even in our own Empire, the results would probably astonish us far more than the above figures have done.

Notes to Chapter XV.

On the dissemination of fungi, the reader will find Fulton, "Dispersal of the Spores of Fungi by the Agency of Insects," *Ann. Bot.*, Vol. III., 1889, p. 207, and Sturgis, "On Some Aspects of Vegetable Pathology and the Conditions which Influence the Dissemination of Plant Diseases," *Botanical Gazette*, Vol. XXV., 1898, p. 187, both useful papers. Further information will be found in Zopf, *Die Pilze*, Breslau, 1890, pp. 79-95 and 228, and Wagner, "Ueber die Verbreitung der Pilze durch Schnecken," in *Zeitschr. f. Pflanzen Krankh.*, 1896, p. 144. The estimates as to losses due to epidemics are taken from Watt, *Agricultural Ledger*, Calcutta, 1895, p. 71; Balfour, *The Agricultural Pests of India*, London, 1887, pp. 13-15;

Eriksson and Henning, *Die Getreideroste*; the publications of the U.S. Department of Agriculture, *The Kew Bulletin*, and elsewhere. The reader will find further examples in Massee, *Text-Book of Plant Diseases*, 1899, pp. 47-51. Both these subjects are well worth further attention, and I know of no complete account of them.

CHAPTER XVI.

THE FACTORS OF AN EPIDEMIC.

Illustrations afforded by the potato disease—The larch disease—The phylloxera of the vine.

WHEN we come to enquire into what circumstances bring about those severe and apparently sudden attacks on our crops, orchards, gardens, and forests by hosts of some particular parasite, bringing about all the dreaded features of an epidemic disease, we soon discover the existence of a series of complex problems of intertwined relationships between one organism and another, and between both and the non-living environment, which fully justify the caution already given against concluding that any cause of disease can be a single agent working alone.

The statement of prophecy that a particular insect or fungus need not be feared, because it is found to do so little harm in particular cases or districts examined, will thus be seen to be a

dangerous one: any pest may become epidemic if the conditions favour it!

In 1844 and 1845 the potato disease assumed an epidemic character so appalling in its effects that it is no exaggeration to say that it constituted a national disaster in several countries. It was stated at the time that this disease had been known for some time in Belgium, in Canada and the United States, in Ireland, in the Isle of Thanet, and in other parts of the world. Similar, but less devastating epidemics have occurred in various years since. It was generally noticed during such epidemics that the plants themselves were full of foliage, surcharged with moisture, and of a luxuriant green colour promising abundant crops. The now well-known spots, at first pale and then brown and fringed with a whitish mould-like growth—the conidiophores of the *Phytophthora*—were observed during the dull cloudy and wet weather, cooler than usual, when the atmosphere was saturated for days together, in July and August. The actual amount of rain does not appear to have been excessive, but most observers seem to agree that dull weather with moist air had succeeded a warm forcing period of growth. So rapidly did the disease run its course that in a few days nearly all the plants were a rotting blackened mass in the fields, and the potatoes dug up afterwards were either already rotten or soon became so in the stores. Further experience has confirmed this, and we now know that the epidemic is very apt to appear in any region where

potatoes are grown on a large scale, in dull moist weather, especially in fields exposed to mists, heavy dews, etc., about July and August, when the foliage is full and turgid. Similarly on heavy wet soils, unless the season is remarkably open and dry; but also on dry light soils in rainy seasons. So evident was this that many believed that the mists and dew brought the disease—harking back to the superstitions of earlier days. We must remember that prior to 1860 the life-history of *Phytophthora* was not known. Since De Bary's proof of the germination of the zoospores and of the infection of the leaves, the course of the hyphae in them and in the haulms, the origin of the conidia, etc., and the confirmation by numerous competent observers of the true fungus nature of this disease, we are now in a position to understand the principal factors of the various epidemics of potato disease.

It is not merely that the potato-fields afford plenty of food for the fungus, and that the dull weather causes the tissues to be surcharged with moisture, owing to diminished transpiration, but the mists and dew—to say nothing of actual rain and the flapping of wet leaves—favour the germination and spread of the zoospores throughout the field. Whether the dull light also favours the accumulation of sugars in the tissues, and the partial etiolation of the latter implies less resistance to the entering hyphae, may be passed over here, but in any case it is clear that we have several factors of the non-living environment

here favouring the parasite and not improving the chances of the host, even if they do not directly disfavour it.

As another instance I will take the Larch-disease, which is due to the ravages of a Peziza (*Dasyscypha Willkommii*) the hyphae of which obtain access by wounds to the sieve-tubes and cambium of the stem, and gradually kill them over a larger and larger area and so ring the tree, with the symptoms of canker described below.

Now the Larch fungus is also to be found on trees in their Alpine home, but there it does very little damage and never becomes epidemic except in certain sheltered regions near lakes and in other damp situations. How then are we to explain the extensive ravages of the Larch disease over the whole of Europe during the latter half of this century? The extensive planting, providing large supplies for the fungus, does not suffice to explain it, because there are large areas of pure Larch in the Alps which do not suffer.

In its mountain home the Larch loses its leaves in September and remains quiescent through the intensely cold winter, until May. Then come the short spring and rapid passage to summer, and the Larch buds open with remarkable celerity when they do begin—*i.e.* when the roots are thoroughly awakened to activity. Hence the tender period of young foliage is reduced to a minimum, and any agencies which can only injure the young leaves and shoots in the tender stage must do their work in a few days, or the opportunity is

gone, and the tree passes forthwith into its summer state.

In the plains, on the contrary, the Larch begins to open at varying dates from March to May, and during the tardy spring encounters all kinds of vicissitudes in the way of frosts and cold winds following on warm days which have started the root-action—for we must bear in mind that the roots are more easily awakened after our warmer winters than is safe for the tree.

It amounts to this, therefore, that in the plains the long continued period of foliation allows insects, frost, winds, etc., some six weeks or two months in which to injure the slowly sprouting tender shoots, whereas in the mountain heights they have only a fortnight or so in which to do such damage. That the lower altitude and longer summer are not in themselves inimical to Larch is proved by the splendid growths made by the trees first planted a century ago. Then came the epidemic of Larch-disease: the fungus, which is merely endemic—*i.e.* obtains a livelihood here and there on odd trees, or groups of trees in warmer or damper nooks—in the Alps, was favoured by the more numerous points of attack afforded to its spores by injuries due to insects—*Coleophora*, *Chermes*, etc.—and frost wounds, as well as by the longer periods of moist dull weather, and the longer season of foliation. Moreover, as time went on almost every consignment of young Larch-trees sent abroad was already infected. Here again, then, we find the factors

of an epidemic consisting in events which favour the reproduction and spread of a fungus more than they do the well-being of the host.

As a third illustration I will take the case of an insect epidemic. In 1863 a disease was observed on vines in the South of France which frightened the growers as they realised its destructive effects: the roots decayed and the leaves turned yellow and died before the grapes ripened, and such vines threw out fewer and feebler shoots the following year, and often none at all afterwards. In 1865 the disease was evidently becoming epidemic near Bordeaux, and in 1868 it was shown to be due to an insect, *Phylloxera*, the female of which lays its eggs on the roots, where they hatch. The louse-like offspring sticks its proboscis into the tissues as far as the central cylinder. The irritated pericycle and cortex then grow and form nodules of soft juicy root-tissue at which the insect continues to suck. Rapid reproduction results in the majority of the young rootlets being thus attacked, and since they cannot form their normal periderm and harden off properly they rot, and admit fungi and other evils, in consequence of which the vine suffers also in the parts above ground.

Evidence that the general damage is due to the diminished root-action is found in the peculiarly dry poor wood formed in the "canes" of diseased plants.

By 1877 the epidemic had spread to the northern limits of the French vineyards, and by 1888 half the vines in the country were attacked,

and the yield of wine reduced from half a million hectolitres to 50,000 only. Meanwhile the disease had spread to Italy, Germany, Madeira, Portugal, and even to the Cape, though not in epidemic form as in the Bordeaux centre whence it spread.

Now it appears that *Phylloxera* has long been in the habit of doing damage to vines in America, where, however, it attacks the leaves, on which it makes pocket-like galls, rather than the roots. Moreover, there are species and varieties of American vines which, even when planted in Europe, do not suffer at all from this insect at the roots, either because the rootlets do not push out at the same season as those of the European form, or because they form wood more rapidly and completely, or secrete resinous and other matters distasteful to the insect in greater quantity and are thus capable of healing the wounds, or in some other way they do not respond to the attack or suit the insect. In any case the attack on the leaf rather than the root seems to be the exception in European vineyards and the rule in American species, and we appear to be face to face with a problem of specific predisposition to this particular malady. That the resistant properties of the vines of America—not all, only particular species and varieties are thus "immune"—can be utilised has been proved by European growers; and not only so, for Millardet and others have shown that the European vine grafted on to these resistant stocks suffer less than when on their own roots. It has

also been shown that hybrids can be obtained which are resistant.

But the most curious point of all is that *Phylloxera* was itself a native of America, and came thence to Europe. It had played its part with certain fungi in ruining all the attempts to introduce the European vine into America many years ago. A recent authority on the evolution of American fruits writes as follows:

"All the most amenable types of grapes had long since perished in the struggle for existence, and the types which now persist are necessarily those which are, from their very make-up or constitution, almost immune from injury, or are least liable to attack . . . the *Phylloxera* finds tough rations on the hard, cord-like roots of any of our eastern species of grapes. But an unnaturalised and unsophisticated foreigner, being unused to the enemy and undefended, falls a ready victim; or if the enemy is transported to a foreign country the same thing occurs."

Further proof that it is in the "constitution" of the European vine that the want of resistance to *Phylloxera* resides, is furnished by the fact that in California and the Pacific states the European vine was introduced with more success, but is now suffering badly because *Phylloxera* has spread there also. It must not be overlooked, however, that we are as yet very ignorant of all that is implied in the word "constitution" as used above.

If we enquire further why the *Phylloxera*

epidemic was so much worse in the Southern vineyards than in the more Northern ones of Germany, the opinion seems to prevail that the warmer climates favour the insect. Further, it appears that, in Italy, the vines in loose open soil, provided it is equally rich in mineral food-materials and offers no disadvantages as regards drainage, suffer less than those in closer soils, the reasons alleged being that the young roots can push out more rapidly and widely, and so obtain holdfasts with greater distances between them.

Notes to Chapter XVI.

The student may obtain further information on the history of the Potato disease by consulting the following: Berkeley, "Observations, Botanical and Physiological, on the Potato Murrain," *Journal of the Horticultural Society*, Vol. I., 1846, p. 9; De Bary, *Die Gegenwärtig herrschende Kartoffel Krankheit*, etc., Leipzic, 1861; and the pages of the *Gardeners' Chronicle* from 1860-1900.

For the Larch disease he should consult Hartig, *Unters. aus der Forst. Botanischen Inst. München*, B. I., 1880; and Willkomm, *Microscop. Feinde des Waldes*, B. II., 1868.

For *Phylloxera* the literature is chiefly in the *Comptes Rendus* and other French publications since 1875, and in the Reports of the U.S. Dept. of Agriculture.

For a summary of the facts concerning the life-histories of the parasites referred to above, see Frank, *Krankheiten der Pflanzen*, and Marshall Ward, *Diseases of Plants*, p. 59, and *Timber and Some of its Diseases*, London, 1889, chapter X.

Also Marshall Ward, "On some Relations between Host and Parasite in certain epidemic Diseases of Plants," *Proc. Roy. Soc.*, Vol. XLVII., 1890, pp. 393-443; and "Illustra-

tions of the Structure and Life-history of Phytophthora infestans," *Quart. Journ. Microsc. Soc.*, Vol. XXVII., 1887, p. 413; also Marshall Ward, "Researches on the Life-history of Hemileia vastratrix," *Journ. Linn. Soc.*, Vol. XIX., 1882, p. 299; and "On the Morphology of Hemileia vastatrix," *Quart. Journ. Microsc. Soc.*, 1881, Vol. XXI., p. 1.

CHAPTER XVII.

REMEDIAL MEASURES.

Preventible diseases — The principles of therapeutics — Powders and their application — Spraying with liquids — Nature of chemicals employed — Employment of epidemics and natural checks — The struggle for existence.

It may be said that in no connection is the proverb "Prevention is better than cure" more applicable than with this subject, and undoubtedly the best utilitarian argument that can be used in favour of a thorough study of the causes of disease is that only by understanding these causes is there any hope of avoiding the exposure of crops, garden plants, forest trees, etc., to the attacks of preventible diseases. Moreover, only an intelligent appreciation of the causes of a disease will enable the cultivator to take steps to mitigate their effects when once the damage has begun its course. Every cultivator learns by experience or by precept that there are some

things he must avoid in dealing with certain plants, or otherwise they will not succeed; in other words they will succumb to diseased conditions and die. It is partly owing to the want of systematisation of this knowledge, and its extension in other directions, that such extraordinary blunders are made in ignorant practice, and trees for instance are planted in low-lying frost beds which would succeed in slightly higher situations, or seeds subject to damping-off are sown in beds rife with the spores of *Peronospora* or *Pythium*, and so forth.

Many diseases, however, are not preventible in the present state of our knowledge, or prevailing conditions are such that the risk must be run of endemic diseases gradually becoming epidemic, and thus the natural desire for some means of checking the ravages of some pest or another has led to innumerable trials to minimise the effects by prophylactic measures. The procedure almost invariably followed where parasites are concerned, consists in either dusting the plants with some chemical in the form of a powder, or spraying it with a liquid, or occasionally in enveloping the plant in some gas, in each case poisonous to the insect- or fungus-pest. The principal rules to be observed are: (1) the poison employed must be sufficiently strong or concentrated to kill the parasite, but not sufficiently powerful to injure the host; (2) it must be applied at the right period, as suggested by a knowledge of the life-history of the fungus or insect in question.

Obviously it is of no use to apply such topical remedies to a parasite while it is spending the greater part of its life inside the tissues of the host. Further, questions of expense of the materials employed and of the labour of applying them help to limit the adoption of such measures.

Among the various kinds of powders employed, finely divided sulphur, or a mixture of sulphur and lime, have been used with success in some cases—*e.g.* against Hop mildew and other epiphytic Erysipheae, and against red spider, aphides, etc., the gaseous sulphur dioxide evolved being the efficacious agent. In other cases pyrethrum or tobacco powder, wood ashes, etc., have been employed against insects. Such powders are applied by hand or by means of bellows, and are very easily manipulated in most cases, though, like all such applications, the dangers of concentration at particular spots owing to uneven distribution, or of dilution and washing off by rain, have to be incurred.

Far more numerous are the various liquids which have been employed for washing, spraying, or steeping the affected parts of diseased plants. Water alone, or aqueous decoctions or emulsions of various kinds—*e.g.*, quassia, tobacco, soap, or aloes, have been widely employed against insects such as green fly, red spider, etc. In greenhouses, where the leaves can be washed by hand or thoroughly syringed, and the concentration and time of action thoroughly controlled, such liquids

are often serviceable, but great practical difficulties are apt to interfere with their use in the open field.

The principal liquids employed against fungi have been copper sulphate and other metallic compounds (Bordeaux mixture, Eau Céleste, etc.), various compounds of arsenic (*e.g.* "Paris green"), potassium sulphite, permanganate, etc., and emulsions of carbolic acid, petroleum, and such like antiseptics, for the exact composition of which the special treatises must be consulted. Some of these, especially Bordeaux mixture, have been experimented with on a very large scale, especially in America, and various forms of spraying machines have been introduced for dealing with large areas.

It is clear that these spraying operations are more particularly adapted to field crops such as Turnips, Hops, Vines, Potatoes, and to garden and greenhouse plants than to woods and plantations; as a rule they cannot be applied to forest trees—though they have been used in orchards—or to roots, seeds, and other parts in the soil, and many special forms of treatment have been devised for particular cases of these kinds.

One of the oldest of these is the steeping of grain in solutions of copper, or in hot water, just before sowing, and the practical eradication of Bunt and, partially, of Smut is due to this practice, which has lately been adapted to potatoes, the principle being that the parasitic germs shall

be killed while still adhering to the outside of the seeds, tubers, etc., before germination. "Finger and Toe" due to *Plasmodiophora* has been successfully dealt with by the application of lime, but we do not know whether the effect is owing to indirect actions in the soil, to direct actions on the plasmodia, or to the increased production of root-hairs induced by liming.

Phylloxera has been treated by plunging into the soil near the roots small blocks of some slowly-soluble medium, such as gelatine, impregnated with carbon-bisulphide, the volatile fumes of which kill the insect, and even more drastic remedies have been tried along similar lines. In America orchard trees infested with insects or fungi have been covered one by one with light tents, and the vapours of prussic acid, burning sulphur, and other poisons allowed to act inside the tent. In all such cases it must be remembered that uncontrolled ignorance of the properties of poisons on the part of the operator may lead to disaster, and the same applies to the much easier treatment of greenhouses, and cases where poisoned food is laid about for insects or vermin.

Attempts, not altogether unsuccessful on the small scale, have also been made to introduce epidemic diseases among rats, mice, and locusts and other insects, by inoculating some of them with parasitic bacteria or fungi (*Empusa*, *Isaria*, etc.), and then allowing them to run loose in the hope that they will communicate the disease to their fellows.

The introduction of lady-birds into districts infested with Coccideae and similar pests which they devour, is also recorded as successful, as also the importation of birds into forests plagued with caterpillars. It must not be over-looked, however, that man's interference with the existing balance of events in the natural struggle for existence is occasionally disastrous, as witness the results of importing rabbits into Australia, goats into the Canary Islands, and sparrows in various countries. Darwin's well-known illustration of the inter-relations between clover, bees, field-mice, and cats (*Orig. of Species*, 6th ed., 1876, p. 57), which shows the astounding probability of the dependence of such a plant on the number of cats in the neighbourhood, well illustrates the situation.

Mere mention must be made of other special treatments.

Caterpillars and larger animals are often picked by hand or their natural enemies—*e.g.* birds, are encouraged in forests. Locusts are caught in nets, trenches, etc., and buried. Woodlice, slugs, etc., are often trapped by laying attractive food such as carrots and overhauling the traps daily: similarly with earwigs. Rings of tar round tree stems have been employed to prevent caterpillars creeping up them.

American Blight has been treated by rapidly flaming the stems. Syringing with hot water has also been employed for vines affected with mildew, mealy bug, etc.

With regard to the alleged immunity from devouring insects of certain poisonous plants, it has been pointed out that *Pangium edule*, which abounds in prussic acid, is infested with a grub, and ivy is occasionally eaten by caterpillars.

Another point as regards insect pests is the well-known destructive effect of a cold, wet spring on the young larvae. The use of cyanide of potassium requires especial care, but has been described as easily carried out with success in greenhouses.

It seems probable that lady-birds, the larvae of wasp-flies and lace-wings, and ichneumon-flies as well as wrens can keep down aphides.

For an example of the treatment of a complex case of "chlorosis" with mineral manures, the reader may consult the *Gardeners' Chronicle*, 1899 (July), p. 405. Many similar cases have been recorded, but it should not be overlooked that very complex inter-relations are here involved.

Charlock has been successfully dealt with by applying 5 lbs. of copper sulphate in 25 gallons of water to each acre of land while the weeds are young.

In all these cases the guiding idea is derived from accurate knowledge of the habits of the insect, fungus, or pest concerned, and obviously the procedure must be timed accordingly. It is a particular case of the struggle for existence, where man steps in as a third and (so to speak) unexpected living agent.

It is clear from our study of the factors of an epidemic that one of the primary conditions which

favour the spread of any disease is provided by growing any crop continuously in "pure culture" over large areas. This is sufficiently exemplified by the disastrous spread of such diseases as Wheat-rust, Larch-disease, Potato-disease, Phylloxera, Hop-disease, Sugar-cane disease, Coffee-leaf disease, and numerous other maladies which have now become historic in agricultural, planting, and forest annals. Providing the favourite food-supply in large quantities is not the only factor of an epidemic, but it is a most important one in that it not only facilitates the growth and reproduction of a pest, but affords it every opportunity of spreading rapidly and widely.

Moreover, Nature herself shows us that such pests are kept in check in her domain by the struggle for existence entailed by innumerable barriers and competitors. As matter of experience also it is found that rotation of crops, planting forests of mixed species, and breaking up large areas of cultivation into plantations, fields, etc., of different species afford natural and often efficient checks to the ravages of fungus and insect pests. Over and over again it has been found that a fungus or an insect which is merely endemic so long as it is isolated in the forest, where its host is separated from other plants of the same species by other plants which it cannot attack, becomes epidemic when let loose on the continuous acres so beloved of the planter. And the same reasoning applies to the success of such pests on open areas from which the birds or other enemies of the pest

have been driven. True, we cannot always trace the tangled skein of inter-relationships between one organism and another in Nature: the recognition of the principle of natural selection and the struggle for existence is too recent, and our studies of natural history as yet too imperfect to lay all the factors clear, but no observant and thoughtful man can avoid the truth of the general principle here laid down. The history of all great planting enterprises teaches us that he who undertakes to cultivate any plant continuously in open culture over large areas must run the risk of epidemics.

Notes to Chapter XVII.

The principal literature, now very voluminous, on this subject is contained in the publications of the U.S. Department of Agriculture from 1890 onwards. See especially *Bulletins*, Nos. 3, 6, and 9; *Farmers' Bulletin*, No. 91, 1899; and *The Journal of Mycology* during the same period. See also Lodeman, *The Spraying of Plants*, London, 1896. A summary of the principal processes will be found in Massee, *Text-Book of Plant Diseases*, pp. 31-47.

With regard to the history of the subject, which still needs writing, the reader should not overlook Roberts, "On the Therapeutical Action of Sulphur," *St. George's Hospital Reports*, date unknown, but subsequent to the following: Berkeley, *Introduction to Cryptogamic Botany*, 1857, p. 277, with references. These are, I believe, with the references to steeping of wheat in De Bary, *Unters. über d. Brandpilze*, Berlin, 1853, among the first attempts to utilise such remedies.

Further facts will be found in the pages of the *Gardeners' Chronicle*, especially since 1890, and in *Zeitsch. f. Pflanzenkrankheiten* since 1891.

CHAPTER XVIII.

VARIATION AND DISEASE.

Predisposition and immunity—Pathological conditions vary—Hardy varieties—"Disease-proof" varieties—Disease dodging—Thick skins—Indian wheats, etc. Cell-contents vary—Citrus, Cinchona, Almonds, etc. Double ideals in selection—Cultivation of pest and host-plant—Variations of fungi—Bacteria—Specialised races—Difficulties—Experiment only will solve the problems.

THE numerous and often expensive failures in the application of any prophylactic treatment, have proved an acute stimulus to the research for other ways of combating the ravages of plant diseases. It is a matter of every-day experience that particular varieties of cultivated plants may suffer less from a given disease than others in the same district; also that one and the same species may suffer badly in one country and not in another—*e.g.* the Larch in the lowlands of Europe as contrasted with the same tree in its Alpine home,

and the various species of American Vines in Europe.

These matters, in the hands of astute observers, are turning the attention of cultivators and experts to new aspects of the question of plant diseases, namely, the possible existence of immunity, and the breeding of disease-proof varieties; and the existence on the part of the host plant of predispositions to disease which may depend on some factors in the plant or in the environment over which it is possible to exercise control, or which, if known, can be avoided.

The matter is complicated by the recent demonstration of the fact that parasites also vary and can adapt themselves to altered conditions, as is shown by the history of the coffee-leaf disease (*Hemileia*) in Ceylon, and by Eriksson's results with Wheat-rusts (*Puccinia*) and various experiments with *Coleosporium* and other Uredineae; but there are good grounds for concluding that hybridisation, grafting, and selection of varieties may do much towards the establishment of races which will resist particular diseases, as shown by Millardet's experiments with Vines, and the results obtained by Cobb and others with Wheat.

The great difficulty with so-called "disease-proof varieties" is to test them under similar conditions in different countries, and for a sufficient period of time. A particular race of Wheat may behave very differently in Norfolk, Devonshire, and Northumberland, and the recent introduction of the purely experimental method in this connection is

a marked advance. However rough the experiments may of necessity have to be, it is only by such means that data can be gradually accumulated.

Having now obtained some insight into the factors concerned in disease, let us enquire further into the bearing of variation on these. It is evident that pathological conditions may vary; indeed they are themselves symptoms of variation, as we have seen. The history of all our cultivated plants shows abundantly that many of the variations obtained by breeding in our gardens, orchards, fields, etc., involve differences of response on the part of the plant to the very agencies which induce disease. Every year the florists' catalogues offer new "hardy" varieties; but a hardy variety is simply, for our present purpose, one which succumbs less readily to frost, cutting winds, cold damp weather, and so forth. If anyone doubts that hardy varieties have been gradually bred by selection, I refer him to the evidence collected by De Candolle, Darwin, Wallace, Bailey and others. When we come to enquire into the causes of "hardiness," however, difficulties at once beset us. The adaptation may express itself in a difference in the time of flowering or leafing, the exigencies of the season being "dodged," as it were, in a manner which was impossible with the original stock, as appears to have occurred with Peaches in America; or it may be expressed in deeper rooting, as is said to be the case in some Apples, or in the acquirement of a more deciduous habit, or in actually increased resistance to low temperatures.

In such cases we cannot trace what alterations have occurred in the cells and tissues concerned, though we may be sure that some changes do occur.

No experienced cultivator doubts that some varieties of Potato, Wheat, Vine, Chrysanthemum, etc., suffer more from epidemic diseases than others, and our yearly catalogues furnish us with plenty of promises of "disease-proof" varieties. Here also we may imagine several ways in which a particular variety may resist or escape the epidemic attacks of fungi which in the same neighbourhood decimate other varieties. If we could breed a variety of the Larch which opened its buds later than the ordinary form in our northern plains, the probability of its escaping the Larch-disease would be increased in proportion to the shortness of the period of tender foliation described on p. 153. It has been claimed for certain varieties of Wheat that increased thickness of the cuticle and fewer stomata per square unit of surface have diminished the risk of infection by Rust fungi, and for certain varieties of Potato, that the thicker periderm of the tuber protects them against fungi in the soil. That certain thick-skinned Apples, Tomatoes, and Plums pack and store better than those with a more tender epidermis seems proved—that is to say, they suffer less from fungi which gain access through bruises and other wounds; but it cannot be said that any convincing proof is yet to hand explaining in detail why some races of wheat

resist Rust, or why the roots of American Vines suffer less from *Phylloxera* than others.

One of the most extraordinary cases known to me in this connection is the unconscious selection on the part of native Indian cultivators, perfectly ignorant of the principles involved, of spring and autumn forms of Rice, Wheat, Castor Oil, Sugar Cane, Cotton, and other crops. "It has been estimated that Bengal alone possesses as many as 10,000 recognisable forms of rice." Now there is not the slightest ground for doubt that these have been unconsciously bred from the semi-aquatic native species during the many centuries of Indian agriculture, and nevertheless they have, among other peculiar races, some hill-breeds which they cultivate on dry soils and without direct inundation. That is to say, they possess tropical and temperate races differing far more than our spring and summer wheats.

Something has been gained, then, if we can show that there is nothing absurd or hopeless in the search for disease-proof or resistant races, and I think this can be done. We must not forget that the ideal usually set before himself by a breeder of plants has hitherto been almost exclusively some standard of size, form, colouring, and so forth, of the flower, or of taste and texture of the fruit, tuber, etc., though experiments with *Cinchona*, with brewery yeasts, and other plants remind us that variations in other directions have been attended to also.

Now it is obvious that in breeding sour limes

and sweet oranges the cultivator is selecting, and intensifying by selection, very different metabolic processes in the cell: he can test the results of these, and so the selection proceeds.

The question is, Could he select at the same time those variations in cell activity which express themselves in properties of the flower, fruit, foliage, etc., he desires, as well as such variations as aid the cells in repelling fungi, insects, or exigencies of the non-living environment?

That more or less disease-proof varieties could be selected if that object alone were kept in view can hardly be doubted; plenty of examples exist already which show that the necessary variations to work upon exist in just those secretions of protoplasm, etc., which we have seen are concerned in repelling or attracting parasites.

The Sweet Almond has lost the power of producing amygdalin and prussic acid in its cells; Cinchona plants vary immensely in the quantity of quinine formed, and in European hot-houses may even form none at all; some varieties of Maize have sugar and dextrine instead of starch in their endosperms, or coloured instead of clear sap in the aleurone layer, and recent researches prove that they can transmit these peculiarities to hybrid offspring; non-poisonous bacteria have frequently been got from poisonous species simply by cultivation under special conditions, and pigmented forms can be bred into non-pigmented races.

But we see that the difficulty of selection is

increased in the case postulated above, because two ideals are to be worked up to, and they may conceivably be incompatible. Not necessarily so, however, for breeders have solved such problems before in obtaining early *and* heavy cropping races of potatoes, wheat, etc., sweet *and* large grapes, strawberries, etc., hardy *and* brilliant flowers, and so forth.

There is, however, another aspect of this question of variability in organisms in this connection to be considered. Ever since cultivation began man has probably been cultivating not only the crops he desires, but also the pests which infest them, and if variation of his chosen plants occurs—and no one will deny that—surely variation of the fungi and insects which live on them also takes place. That this is so can be demonstrated, though, since it is not part of my theme to go into the question of peculiarities of species and races of parasites, the subject must here be passed over with a few remarks only.

Recent researches have shown not only that fungi vary immensely in form and morphological characters according to the amount and kind of food-materials put at their disposal, thus bringing the whole question of polymorphism into the domain of experimental physiology, but that their capacities for infection, spore formation, etc., are also capable of variation and are dependent on the quality and quantity of food supplies, water, as well as on the temperature, illumination,

and other factors of the environment. This is true of parasites as well as of saprophytes. *Botrytis* forms conidia only in darkness and in moist air. Klebahn found that a *Puccinia* growing on *Digraphis* infected *Polygonatum* readily and completely, *Convallaria* imperfectly, whereas if sown on *Majanthemum* it only just infected the plant and then remained sterile, while it refused to infect *Paris* at all. Magnus has shown that *Peronospora parasitica* can only infect meristematic tissues, and that when it co-exists with *Cystopus* on *Capsella*, as is usually the case, it enters the latter plant by infecting the gall-like pustules of hypertrophied tissue induced by that parasite. Numerous parasitic fungi can only penetrate particular parts of plants. For instance, the *Ustilago* of wheat can only infect the young seedling, and grows for weeks as a barren mycelium, only becoming a dominant fungus in the endosperm. Numerous other examples could be given, but these suffice to show some of the ways in which the nature of the food substratum supplied by the host affects the fungus. It is obvious that if the nature of this food changes, the fungus is also affected, and no doubt this is the principal reason why Rust-fungi, for instance, vary so much in their vigour and reproductive power on different wheats and grasses, though the other factors of the environment must also be of influence on them as well as on the hosts.

But—and this is the second point—modern

research is also showing that the various species of Rust-fungi have split up into different varieties or specialised races, according to the particular host plants they inhabit. For instance there are special varieties or races of the particular species known as *Puccinia graminis*, the wheat rust, each of which grows well on various kinds of grain and grasses but refuses to infect others. Thus, the variety which infects Wheat refuses to infect Barley or Oats, while that variety which grows on Rye will not take on Wheat and so forth. Now it is important to notice that these specialised races are indistinguishable one from another by their visible microscopic characters: they are all botanically of the species *Puccinia graminis* which forms its æcida on the Barberry. We must therefore conclude that we have here the same phenomenon as that met with in culture-races of bacteria which, having been fed for several generations on media rich in proteids, refuse to grow on media rich in carbohydrates, or when attenuated races are developed by culture under special conditions.

Now since such physiological races as I have described are by no means confined to *Puccinia* but are also known in *Melampsora*, *Gymnosporangium* and other fungi, we must conclude from this and from what we know of variation in plants and animals generally, that variation and adaptation are common among parasites, insects as well as fungi.

These considerations will serve to show more-

over that the question of breeding disease-proof varieties of our cultivated plants is complicated by the danger of our breeding at the same time adapted races of their pests. It appears at first sight extremely improbable that we should escape the danger by breeding from those specimens of our plants which have best survived a fungus epidemic. Still, it must not be forgotten that "hardy varieties," and races adapted to other exigencies of the non-living environment, have been bred by selection—and nevertheless this variable non-living environment is always with us. The matter is therefore simply and solely one of experiment, and the retort that a disease-resisting variety of any particular plant has not yet been raised is no more valid than the objection that a true blue primrose has not yet been obtained: whether the same remark can be made with regard to any hope of a *disease-proof* plant may be another matter, but in any case it must be made more cautiously in the light of our present experience.

Notes to Chapter XVIII.

The reader will find more on this subject in Bailey's *Survival of the Unlike* and the literature quoted in the notes to Chapter VIII.

For varieties of Indian Wheats, etc., see Watt, *Agricultural Ledger*, Calcutta, 1895.

For a discussion on so-called "Disease-proof Wheats" consult Eriksson & Henning, *Die Getreideroste*.

Magnus' paper is in the *Berichte der Deutschen bot. Gesellsch.*, 1894, p. 39.

Concerning physiological races and adapted varieties of *Puccinia*, etc., see Eriksson, "A General View of the Principal Results of Swedish Research into Grain Rust," *Botanical Gazette*, vol. 25, 1898, p. 26.

For an account of Wheat-rust see Marshall Ward, "Illustrations of the Structure and Life-history of *Puccinia graminis*, etc.," *Ann. of Bot.*, 1888, Vol. II., p. 215.

CHAPTER XIX.

SYMPTOMS OF DISEASE.

Discolorations—Pallor—Etiolation—Laying of Wheat—Chlorosis—Yellowing—Albinism—Variegation—Uprooting, Exposure and Wilting of seedlings.

EVERYBODY knows in a general way when the geraniums in the window pots are drooping from want of water, or when the young Wheat is sickly, or the Pear-trees "blighted," and we have now to see how far we can systematise the knowledge that has been gained in course of time regarding the signs which sick plants exhibit.

Pallor.—Under this heading, which includes all cases where the normal healthy green colour is replaced by a general sickly yellow or pale hue, ultimately resulting in death of the parts if not arrested, we have several totally distinct diseases of the chlorophyll apparatus, each recognised by the co-existence of other subordinate symptoms. The principal varieties of pallor usually met with are the following:

Etiolation is due to insufficient intensity of light, the pale sickly yellow organs being unusually watery and deficient in vascular tissue, the internodes abnormally long and thin, and the leaves generally reduced in size, or, in some plants also "drawn."

Forced Endive, Rhubarb, Asparagus, and earthed Celery afford examples of etiolation purposely induced. The want of light causes the true chlorophyll colouring matter to remain in abeyance, and consequently the plant as a whole suffers from carbohydrate starvation.

Laying of Wheat and other cereals is a particular case of etiolation. The seeds having been sown too thickly, the bases of the haulms, owing to the etiolation and consequent lack of carbohydrates, suffer from want of stiffening tissues, and the top-heavy plants fall over.

False etiolation depends on a similar abeyance of the chlorophyll, but in this case due to too low a temperature. It is often seen in Wheat and other monocotyledons when the young leaves unfold in cold weather in spring. The symptoms of "drawing" and tenderness are however absent.

Pallor due to too intense illumination must be kept sharply distinct from etiolation, the pale green or yellow hue being here due to the destruction of the chlorophyll by insolation, and the accessory symptoms of "drawing" are wanting.

Chlorosis is a form of pallor where the chlorophyll grains themselves are fully developed, but their green pigment remains in abeyance owing to a deficiency of iron in the soil, and can often be

cured by adding traces of a ferrous salt. The distinction between *Icterus*, where the organs are only yellow, and *Chlorosis* proper, where they are nearly white cannot always be maintained. In the typical case only those organs whose cells are still young can become green on adding iron.

Yellowing or *False Chlorosis* may be experimentally induced by too much carbon-dioxide in the atmosphere. It also often ensues when the roots of plants in the open are waterlogged, owing to the stagnant water not only driving air from the root-hairs but accumulating dissolved substances which poison the plant. Trees frequently thus suffer from "wet feet" when their roots have penetrated down to a sodden impervious subsoil.

Yellowing accompanied by *Wilting* is a predominant symptom in most cases where transpiration is more active than root-absorption beyond a certain limit, as is well known in cases of prolonged drought. It may also be caused in evergreens by the foliage transpiring actively in bright January weather, for instance, while the ground is frozen and the chilled root-hairs cannot absorb.

In other cases similar appearances are traceable to insects devouring the roots, *e.g.* wireworms, and the malady is sometimes enhanced by their accumulations so fouling the wet soil that the roots die off, owing to want of oxygen and to the excess of carbon-dioxide and poisonous matters.

Yellowing may also result from the presence of poisonous or acid gases in the atmosphere or soil, such as chlorine, hydrochloric acid, sulphurous

acid, etc., in the neighbourhood of chemical works, or from the escape of coal-gas in streets, etc., points of importance in connection with the use of fungicides and insecticides.

Yellowness is the prevailing symptom in many cases of fungus attack of the roots or collar of the plant, the resulting stoppage of transpiration being also sometimes supplemented by rotting of the roots, and the consequent deprival of oxygen and accumulation of foul gases. In other cases Fungi, and even Bacteria, have been found to have made their way into the principal vessels, the lumina of which they stop up, thus reducing the transpiration current.

Certain insects may also induce a general yellowing and wilting of plants by entering or destroying the tissues concerned in the transpiration—*e.g.* *Oscinis*, the Frit Fly, and *Cecidomya*, the Hessian Fly, which attack young winter wheat within the sheaths and cause the plants to turn yellow and wilt.

Albinism and *Variegation* are apparently due to causes totally different from any yet mentioned. Church's analyses have shown that albino leaves contain more water and less organic matter than green ones of the same plants, but not necessarily less ash constitutents. The composition of the ash points to there being more potash and less lime in the white organs than in the green ones, and, speaking generally, the former are related to the latter much as young leaves are related to mature ones.

The whole matter is complicated by the behaviour of certain *variegated* plants—*e.g.* Ribbon grass, *Calla*, *Abutilon*, which are usually regarded as partial albinos.

Meyen showed long ago that such variegated plants, if grafted on green ones, may induce the development of variegated leaves on both scion and stock, and Morren and others have not only confirmed this but have also shown that variegation may be inherited through the seed. Nevertheless some care has to be taken with many of these variegations lest rich soil, bright light, and other favourable treatment favour the restitution of the green colour. These facts may be interpreted in various ways. Some disturbance of physiological functions of the roots, due to unfavourable conditions of soil, may be the cause ; but Beijerinck has lately published some results which show that some of these albino diseases can be induced by inoculating normal plants with the juice of spotted ones even though such juice has been filtered through porcelain, and concludes that a "*contagium fluidum vivum*" of the nature of a transmissible enyzme is the agent which disturbs the physiology of the infected cells.

Koning, while confirming these results in the main, refers them to a micro-organism so small that it traverses the porcelain filter.

Upheaval of seedlings.—This is a common form of injury, resulting in death by drought and exposure, especially in seedling pines, wheat, etc., in soils exposed to alternate freezing and thawing

during spring when there is no snow to protect the plants. The soil freezes during the night, and during the thaw next day water accumulates just below the surface. The freezing is then repeated, and, partly owing to the expansion of the forming ice and partly to the mechanical effect of the ice-crystals in the interstices, the surface of the soil is lifted and draws the roots with it. During the succeeding thaw the soil particles fall away from the lifted root-fibres, and frequent repetition of these processes results in such complete exposure of the roots to the full sun that the plantlet falls over and wilts.

Exposure of roots is also sometimes effected by winds displacing sandy soils liable to shifting in dry weather, and the resulting wilting of the plants thus exposed at their roots may be supplemented by damage due to the repeated impact of the wind-driven sharp grains of sand, which act like a sand-blast and erode the tissues.

In many of the cases given above the principal result is the weakening or destruction of the chlorophyll action. This means a loss of carbohydrates —sugars, starches, etc.—and in so far a starvation of the plant. The injurious effects are quantitative and cumulative: if large areas of foliage are concerned, or if the effect lasts a long time, the plant suffers from loss of food, and may die. In those cases where the effect is due to the cutting off of supplies at the roots, and where the yellowing is a secondary symptom, the disease is more general in character, and recovery is often im-

possible, because the loss of water cannot be compensated, and the results may be further complicated by the gradual penetration of poisonous matter into the cells. It is frequently necessary, though sometimes very difficult, to decide which is the primary and which secondary (or tertiary, etc.) symptoms in the order of their importance, and the diagnosis may be complicated by a number of accessory factors which it is impossible to treat generally.

Notes to Chapter XIX.

The principal cases here described are dealt with in works on plant physiology, and in the works of Sorauer and Frank already referred to.

As regards damage due to uprooting of seedlings by frost, see Fisher, "Forest Protection" (Engl. ed. of Hess' *Forstchutz*), in Schlich's *Manual of Forestry*, Vol. IV., 1895, pp. 439-442.

On Albinism, see Church, "A Chemical Study of Vegetable Albinism," *Journ. Chem. Soc.*, 1879, 1880, 1886.

Beijerinck's results are contained in his paper, "Ueber ein Contagium vivum fluidum," etc. (with English abstract), in *Verhandl. d. Kon. Akad. v. Wetensch, te Amsterdam*, 1898. Koning's paper is in *Zeitschr. f. Pflanzenkrank.*, Vol. IX., 1899, p. 65. See also *Nature*, Oct. 11, 1900, p. 576.

CHAPTER XX.

SYMPTOMS OF DISEASE (*Continued*).

Spotted leaves—The colours of spots—White, yellow, brown, and black spots on leaves—Parti-coloured spots—The browning, etc., of leaves.

Discoloured spots or patches on the herbaceous parts of plants, especially leaves, furnish the prominent symptoms in a large class of diseases, due to many different causes, and although we cannot maintain this group of symptoms sharply apart from the last, as seen from the considerations on *albinism*, it is often well marked and of great diagnostic value. By far the greater number of spot-diseases are due to fungi, but this is by no means always the case. The most generally useful method of subdividing the classes, though artificial like all such classifications, will be according to the colour of the spots or flecks, which, moreover, are usually found on the leaves. It is necessary to note, however, that various conditions may modify the colour of spots on leaves. Many

fungi, for instance, induce different coloured spots according to the age of the leaf or other organ attacked, or according to the species of host, the weather, etc. Moreover the spots due to these parasites are frequently yellow when young and some other colour, especially brown or black, when older.

Scale is the name given to the characteristic shield-like insects (*Mytilaspis*, *Aspidiotus*, etc.) which attach themselves to branches of Apples, Pears, Oranges, Camellias, and numerous other plants, and suck the juices. It is the female insect which has the body broadened out into the "scale," under which the young are brought up. Enormous damage has been done by some forms —*e.g.* the San José scale in the United States.

The superficial resemblances of the patches of eggs of some Lepidoptera to Aecidia and other fungi may be noted in passing—*e.g.* *Bombyx neustria* on Apple twigs, *Aporia Crataegi*.

White or *greyish spots* are the common symptom marking the presence of many Peronosporeae and Erysipheae in or on leaves, *e.g.* *Peronospora Trifoliorum*, *P. parasitica* on Crucifers, etc., and *Sphaerotheca* on Hops; also *Septoria piricola*, *Cystopus*, *Entyloma Ranunculi*, etc.

White spots are also caused by insects such as *Tetranychus* (red spider) on Clover and other plants.

Yellow, or *Orange-coloured Spots.* In cases where these occur on leaves, and in the case of grasses, etc., on the leaf sheaths as well, they

commonly indicate the presence of Uredineae, and sections under the microscope will show the mycelium in the tissues beneath. Species of *Uromyces*, *Puccinia*, etc., in the Uredo state have the spots powdery with spores; *Aecidia* show the characteristic "cluster cups," and so forth. These spots are often slightly pustular, and in some cases markedly so.

Other fungi also induce yellow spots on leaves —*e.g. Phyllosticta* on Beans, *Exoascus* on Poplars, *Clasterosporium* on Apricot leaves, *Synchytrium Succisae* on *Centaurea*, etc.

Yellow spots are also a frequent symptom of the presence of Aphides, of Red Spider, etc. Thus the minute golden yellow spots sometimes crowded on Oak leaves are due to *Phylloxera* punctures.

Yellow patches are formed on the large leaves of *Arisarum* by a species of parasitic Alga, *Phyllosiphon*, which lives in the mesophyll. Many tropical leaves are spotted yellow by epiphytic Algae—*e.g. Cephaleuros*.

It must be noticed that many fungi produce yellow spots or flecks in the earlier stages, which turn brown or black as the fructifications appear, *e.g. Dilophia graminis*, *Rhytisma acerinum*.

The yellow-spotted leaves of *Farfugium grande* (*Senecio Kaempferi*) are so like those of *Petasites* attacked with *Aecidium* in its early stages, that an expert might be deceived until the microscopic analysis was completed.

Red spots, varying from rusty or foxy red to bright crimson, are the symptomatic accompaniment

of several fungi, the former often characterising the teleutospore or aecidium stage of Uredineae—*e.g. Aecidium Grossulariae*—the latter sometimes indicating the presence of Chytridiaceae.

Red spots are also caused by *Gloeosporium Fragariae* on Strawberry leaves, *Polystigma rubrum* on Plums.

Crimson spots on Apple and Pear leaves are also due to *Phytoptus* : they turn brown later.

Brown spots or flecks, varying in hue from dull slaty brown to deep red browns, are a common symptom of Fungus and Insect diseases, the colour often indicating the death of the tissues, rather than any special peculiarity of the action of the parasite. Good examples are furnished by the Potato-disease, and by *Peronospora viticola*, *Sphaerella vitis* and other disease-fungi of the Grape Vine. The teleutospore stage of many Uredineae also occurs in deep brown spots.

Black spots and flecks are exceedingly common symptoms of the presence of fungi, *e.g. Fusicladium* on Apples and Pears, and the pycnidial and ascus stages of many Ascomycetes—*e.g. Phyllachora graminis*. The teleutospore stages of species of *Puccinia*, *Phragmidium*, etc., are also so deep in colour as to appear almost black.

Scab on Pears is due to the presence of *Fusicladium*, which indurates the outer skin of the fruit causing it to crack under pressure from within, and to dry up, the deep brown to black patches of fungus persisting on the dead surface.

Black spots on grasses and sedges are caused

by Ustilagineae, and are commonest in the grain, the soot-like powdery spores (Smut) being very characteristic. *Ustilago longissima* induces black streaks on the leaves. Many of these fungi cause distortions or pustules on leaves and other organs.

Brown and black leaf spots are frequently furnished with concentric contours arranged round a paler or other coloured central point—*e.g. Cercospora* on Beans, *Ascochyta* on Peas.

Brown spots with bright red margins are formed in young Beans by *Gloeosporium*.

Species of *Fumago*, *Herpotrichia*, etc., may cover the entire surface of the leaf with sooty patches, or even weave the leaves together as if with black spider-webs.

Mal nero of the Vine is a particular case of black spotting and streaking of the leaves for which no satisfactory explanation is as yet to hand. As with Chestnuts, Walnuts, and other plants containing much tannin, the dark spots appear to be due to this substance, but whether the predisposing cause is a lack of some ingredients in the soil, or some temperature reaction, or fungi at the roots, is as yet unknown. The most recent explanation puts the disease down to the action of bacteria, but the results obtained by different workers lead to uncertainty.

The "dying back" of leaves, especially of grasses, from the tip, is usually accompanied by a succession of colours—yellow, red, brown, to black—and is a common symptom of parching from summer drought; and spots of similar

colours, frequently commencing at the margins of leaves, are characteristic symptoms of the injurious action of acid gases in the air.

Brown and blackish spots on Pears are caused by a species of *Thrips*.

In many cases the minute spots of Rust-fungi on one and the same leaf are bright orange yellow *(uredo)*, deep brown, or almost purple-black *(teleutospores)*, foxy-red brown (older uredospores), or dead slaty black where the old teleutospores have died off—*e.g. Uromyces Fabae* on Beans, *U. Pisi* on Peas, etc.

Parti-coloured leaves.—The leaves sometimes start shrivelling with red edges, while yellow, red, and finally brown and black blotches appear on the lamina, from no known cause—*e.g.* Vines. In other cases similar mimicry of the autumnal colouring of leaves results from the action of acid gases.

Burning is a common name for all cases where the leaves turn red or red-brown in hot, dry weather, and many varieties are distinguished in different countries and on different plants, because species react dissimilarly. The primary cause is usually want of water—drought.

Foxy leaves are a common sign of drought on hot soils, and the disease may usually be recognised by the gradual extension of the drying and fox-red colour proceeding from the older to the younger leaves, and from base to apex—*e.g.* Hops.

Coppery leaves.—The leaves of the Hop, etc., may show yellow spots and gradually turn red-brown

—copper-coloured—as they dry; the damage is due to *Tetranychus*, the so-called Red Spider. These cases must of course be carefully distinguished from the normal copper-brown of certain varieties of Beech, Beet, *Coleus*, etc.

Silver-leaf.—The leaves of Plum, Apple, and other fruit trees often obtain a peculiar silvery appearance in hot summers, the cause of which is unknown.

Discolorations in the form of confluent yellow and orange patches, etc., resembling variegations, are not infrequently due to the ravages of Red Spider and mites—*e.g.* on Kidney Beans.

Sun-spots.—Yellow spots, which may turn brown or black according to the species of plant affected and the intensity of the action, are often caused by the focussing of the solar rays by lens-like thickenings due to inequalities in the glass of greenhouses, or by drops of water on them or on other leaves, *e.g.* Palms, *Dracaena*, etc. The action is that of a burning glass, and extends throughout the leaf-tissues. Young grapes, etc., may also be injured in this way. Water-drops on the glass can only act long enough to produce such injuries if the atmosphere is saturated. The old idea that a drop on a leaf can thus focus the sun's rays into the tissues beneath is not tenable.

Here again we see that the disease-agencies concerned in producing the symptoms described in this chapter, agree for the most part in so far that the principal effect is generally the disturbance of chlorophyll action in the spots or flecks on

the leaves, and the rendering useless of these areas so far as providing further food-supplies is concerned. The effects may be due merely to the shading action of a parasite—*e.g.* epiphytic fungi—or to actual destruction of the tissues invaded—*e.g.* by endophytic fungi—or the tissues may be burnt, poisoned, etc. In so far the results are again quantitative and cumulative, and the amount of damage depends on the number and size of the spots or other areas affected, and the proportion of foliage involved, as well as the length of time the injurious action is at work. But, again, it must be remembered that several symptoms may co-exist, and matters may be complicated by the spread of the destructive agent, or its consequences, to other parts, and in some cases we are quite uninformed as to the true nature of the disease.

Notes to Chapter XX.

Further information regarding these "leaf-diseases" will be found in special works dealing with the fungi and insects which cause them. In addition to works already quoted, the reader may also be referred for Fungi to Massee, *A Text-book of Plant-diseases caused by Cryptogamic Parasites*, London, 1899; or Prillieux, *Les Maladies des Plantes Agricoles*, 1895. See also Marshall Ward, Coffee-leaf Disease, *Sessional Papers*, XVII., Ceylon, 1881, and *Journ. Linn. Soc.*, Vol. XIX., 1882, p. 299.

The question of "Sun-spots" has been dealt with by Jönnson in *Zeitschr. f. Pflanzenkrankh.*, 1892, p. 358.

CHAPTER XXI.

ARTIFICIAL WOUNDS.

The nature of wounds and of healing processes—Knife wounds — Simple cuts — Stripping — Cuttings—Branch-stumps and pruning—Stool-stumps—Ringing —Bruises.

Wounds.—All the parts of plants are exposed to the danger of wounds, from mechanical causes such as wind, falling stones or trees, hail, etc., or from the bites of animals such as rabbits, worms, and insects, and although such injuries are rarely in themselves dangerous, they open the way to other agencies—water, fungi, etc., which may work great havoc; or the loss of the destroyed or removed tissues is felt in diminished nutrition, restriction of the assimilative area, or in some other way.

We have seen that living cells die when cut, bruised, or torn ; and that the cells next below in a layer of active tissue are stimulated by the exposure to increased growth and division, and at once pro-

duce a layer of cork, the impervious walls of which again protect the living cells beneath. This is found to occur in all cell-tissues provided the cells are still living, and it matters not whether the wound occurs in the mesophyll of a leaf, the storage parenchyma of a Potato-tuber, the cortex of a root or stem, or in the fleshy parts of a young fruit, the normal effect of the wound is in all cases to call forth an elongation of the uninjured cells beneath, in a direction at right angles to the plane of the injured surface, which cells then divide by successive walls across their axis of growth : the layers of cells thus cut off are then converted into cork, by the suberisation of their walls. Further changes may then go on beneath the protective layer of wound-cork thus produced, and these changes vary according to the nature of the cells beneath : the cambium forms new wood, the medullary rays similar rays, cortex new cortex, and so on.

Knife-wounds.— Artificial cuts in stems are easily recognised and soon heal up unless disturbed. Several cases, differing in complexity, are to be distinguished. The simplest is that of a longitudinal, oblique, or horizontal short cut in which the point of the knife severs all the tissues of the stem down to the wood. The first effect usually observed is that the wound gapes, especially if longitudinal, because the cortex, tightly stretched on the wood cylinder, contracts elastically. This exposes the living cortex, phloem and cambium to the air, and such tissues at once behave as already described above : the cells actually cut die,

those next below grow out under the released pressure, and these give rise to cells which become cork. As the growth and cell-division continue in the cells below this thin elastic cork-layer, they form a soft herbaceous cushion or *callus* looking like a thickened lip to each margin of the cut. Each lip soon meets its opposite neighbour, and the wound is closed over, a slight projection with a median axial depression alone appearing on the surface. The depression contains the trapped-in callus-cork squeezed more and more in the plane of the cut as the two lips of callus press one against the other, and sections across the stem and perpendicular to the axis of the cut show that this thin cork, like a bit of brown paper, alone intervenes between the cambium, phloem and cortex respectively of each lip, as each layer attempts to bridge over the interval. If the healing proceeds normally, these layers, each pressing against the trapped cork-film, and growing more and more in thickness, shear the cork-layer and tear its cells asunder, and very soon we find odd cells of the cambium of one lip meeting cambium cells of the other, phloem meeting phloem, and cortex cortex, and the normal thickening of the now fused layers previously separated by the knife goes on as if nothing had happened, the only external sign of the wound being a slight ridge-like elevation, and, internally, traces of the dead cells and cork trapped here and there beneath the ridge. When the conjoined cambium resumes the develop-

ment of a continuous layer of xylem and phloem, no further trace of the injury is observable, unless a speck of dead cells remains buried beneath the new wood, and indicates the line where the knife point killed the former cambium and scored the surface of the wood in making the wound.

Stripping.—Now suppose that, instead of a mere slit with the knife-point, a strip of bark is removed down to the wood. Exactly the same processes of corking and lip-like callus formation at the edges of the wound occur, but of course the occlusion of the bared wood-surface by the meeting of the lips occupies a longer time. Moreover, the living cells of the medullary rays exposed by the wound on the wood-surface also grow out under the released pressure, and form protruding callus pads on their own account. In course of time the wood is again completely covered by the coming together over its face of these various strips of callus, but two important points of difference are found, as contrasted with the simpler healing of the slit-wound. In the first place the exposed wood dries and turns brown, or it may even begin to decay if moisture and putrefactive organisms act on it while exposed to the air ; and, in the second place, the normal annual layer of wood—or layers, as the case may be—formed by the cambium only extends over that part of the stem where the cambium is still intact, and is entirely wanting over the exposed area. Thus, if it takes two years for the cambium to extend

across the wound, a layer of wood will be formed all round the intact part of the stem, from lip to lip of the cut tissues during the first year; then a second annual layer outside this will be formed during the second year, but extending further over the edges of the wound, and nearly complete, because the cambium has now crept further across the wounded surface to meet the opposite lip of cambium; and during the third year, when the cambium has once more become continuous over the face of the wound, the annual wood layer will be complete. But, of course, this last layer covers in the edges of the two previously developed incomplete wood-layers as well as the exposed and brown, dry, or rotten dead face of the wood. It also covers up the trapped-in brown cork and any débris that accumulated in the wound, and this "blemish," though buried deeper and deeper in the wood during succeeding annual deposits of wood-layers, always remains to remind us of the existence of the wound, the date of which can be fixed at any future time by counting the annual rings developed subsequently to its formation. Obviously, also, the deficiency of wood at this place makes itself visible on the outside by a depression.

Cuttings.—When a cutting of *Pelargonium*, Willow, or other plant is made, we have a typical knife-wound, the behaviour of which is very instructive in illustration of plant-surgery, and may be most easily seen by keeping it in damp air instead of plunging it into sand or soil.

All the living cells actually cut or bruised turn brown and die as before; those beneath—*e.g.* the living pith, medullary rays, cambium, phloem, and cortex, grow out under the released pressure and form a callus, the outermost layer of which becomes cork, while those below, abundantly supplied with food-materials, proceed to spread, as if flowing over the surface of the cut wood, and rapidly occlude the wound. Meanwhile new roots are formed adventitiously from the cambium just above the plane of section, and push out through the cortex into the damp air, and if the cutting had been in soil it would now be capable of independent existence. It is important to keep cuttings upright, as the roots only spring from the lower end. Such cuttings can be obtained not only from stems, but also from roots and even leaves.

Callus-formation is not confined to the basal end of a cutting; it has nothing to do with position, but is a reaction to the wound stimuli, independent of light, gravitation, etc. As time goes on, however, the internal organisation of the erect cutting usually reacts on the callus at either end, and roots only rise from the lower one, while shoot-buds may form in the upper one, though it is possible to bring about the formation of buds from the lower end also.

Branch stumps.—A more complex example is furnished by a branch cut off short some distance —say a foot—from the base, where it springs from the trunk. As before, the immediate effect of the

section is the formation of a callus from the cambium, phloem and cortex, which begins to rise as a circular occluding rim round the wood. The transpiration current in the trunk, however, is not deflected into the 12 inches or so of amputated branch, because there are no leaves to draw the water up it, and so the stump dries up and the cortex and cambium die back to the base, leaving the dead wood covered with shrivelled cortical tissues only. This dead stump gradually rots under the action of wet, fungi, and bacteria, and since the pith and heart-wood afford a ready passage of the rot-organisms and their products into the heart of the trunk, we find in a few years a mere stump of touch-wood and decayed bark, which falls out at the insertion like a decayed tooth, leaving a rotten hole in the side of the trunk.

If, however, instead of allowing the basal part of the amputated branch to protrude as a stump, we cut it off close to the stem, and shave the section flush with the normal surface of the latter, the callus formed by the cambium, etc., rapidly grows over the surface, and soon forms a layer of cambium continuous with that of the rest of the stem. The wound heals, in fact, much as if it were a strip-wound, and beyond a slight prominence for a year or two no signs are visible from the outside after the occlusion. Of course these matters depend on the relative thickness of branch and stem, and if much wood is exposed the dangers of rot and a resulting hollow in the stem are increased. It is interesting to note how much thicker the callus lips are at the

sides of the wound than above and below, owing to differences in the distribution of the nutrient materials.

Stool-stumps.—When a tree is felled, the stump may, if the section is close to the ground and kept moist, begin to form a thick rim-like callus round the wood, in which adventitious buds soon make their appearance, and grow out into so-called *Stool-shoots.* The products of assimilation of these, and the stores accumulated in the stump, often suffice to feed the callus sufficiently to enable it to grow over and completely occlude the wound, if the wood surface is not too large, or so long exposed that rotting processes have meanwhile set in.

Ringing.—If the strip of cortical tissues and cambium is removed all round the stem, exposing the wood in a form of a ring, complications may ensue owing to the following circumstances. A well-marked callus appears at the upper edge of the wound, because, the transpiration current up the young wood not being stopped, plenty of water and salts from the soil can reach the leaves; but the nutritive materials supplied by the latter are accumulated at the upper lip of the wound owing to the stoppage there of their descent in the phloem, cortex, etc. No such callus-lip appears at the lower margin of the wound owing to want of these supplies. Consequently the occlusion and healing of the ring-wound only takes place from above downwards, and if the ring of cortical tissues removed is a broad one, the healing may be a long process, or may even be

indefinitely delayed, a thicker and thicker callus projecting over from above. For similar reasons no annual wood layers are formed below, but only above the wound, and thus the branch or tree may die. The latter contingency is the more likely the further up the tree the ringing takes place, owing to the risk of drying up which threatens the exposed wood, and to the consequent interruption of the transpiration current, and the likelihood that lateral shoots below the wound may divert the water to their own leaves. If the ringing occurs low down on a stem, and the environment remains damp, the upper thick callus may put out new roots; the part above the wound then behaves like a cutting. If the ringing is done on a young and vigorous branch of an old tree, the lower lip may receive supplies from the leaves of branches below the wound, or from shoots which spring from adventitious buds close to it, and the wound may heal over normally. Such healing may be rendered more certain by keeping the wounded surface moist—*e.g.* by means of damp moss, and so encouraging the formation of callus-bridges from the medullary rays.

If on ringing a tree or a branch the young wood is removed as well as the cambium and cortical layers, the death of the parts above the wound is almost certain, owing to the stoppage of the transpiration current: the exceptions to this rule depend simply on the existence of other channels of communication, such as internal phloems, very thick sap-wood, and so forth.

Bruises.—If a branch or woody stem is struck sharply, with a hammer, for instance, the bruised cortex, phloem and cambium are killed by the blow, and the general effect is as if these tissues had been removed at that spot by the knife, but with the following complications. The bruised cortical tissues rapidly dry as they perish, and may adhere to the wood below. Consequently the still sound parts bordering on the wound are not released from pressure, but, on the contrary, have to advance towards each other over the surface of the wood under still greater pressures, in part due to the tightening of the whole cortex as the dead parts dry and contract, and in part due to the above-mentioned adherence of the latter to the wood. It results from this that such wounds heal very slowly and badly, and when the killed patch at last ruptures, wound-fungi, insects, and other injurious agencies may get in and do irreparable damage, as has been found to occur in cases where such wounds have been made in striking trees to shake down insects, fruit, etc.

Notes to Chapter XXI.

The essential facts regarding wounds and healing by occlusion are given in Marshall Ward, *Timber and some of its Diseases*, 1889, chapters viii. and ix., and in Laslett, *Timber and Timber Trees*, 1894, chapters iv. and v. More detailed treatment will be found in Frank, *Krankh. d. Pflanzen*, B. I. cap. 2, where the special literature is collected. The reader may also consult Hartig, *Diseases of Trees*, Engl. ed. 1894, pp. 225-269.

CHAPTER XXII.

NATURAL WOUNDS.

Burrows and excavations. Bark-boring—Wood-boring—Wood fungi—Leaf-miners—Pith flecks—Erosions. Skeleton leaves—Irregular erosions—Shot holes. Frost cracks—Strangulations—Spiral grooving.

NATURAL wounds are produced in a variety of ways during the life of the plant, and, generally speaking, are easily healed over by the normal process if the area destroyed is not too large, and the parts remaining uninjured are sufficiently provided with foliage, or with supplies of food-materials stored up in the roots, rhizomes, medullary rays, etc., to feed a vigorous callus.

The nature of such wounds and the mode of healing are explained by what we know of artificial wounds, and it only remains to point out that the principal danger of ordinary wounds is not so much the direct traumatic action, because the simpler organisation of the plant does not involve matters connected with shock, loss of

blood, etc., as in animals; the danger consists, rather, in their affording access to other injurious agents, especially fungi, and the treatment of wounds frequently resolves itself into cutting or pruning in order to get clean surfaces which can heal readily.

Wounds on leaves imply loss of foliar surface—*i.e.* of chlorophyll action—and the remarks on page 193 apply.

Burrows may be taken as comprising all kinds of tunnel-like excavations in the various organs of plants, including those cases where insects burrow into hollow stems of grasses, etc., as indicated by the perforations they make in the outer tissues.

Bark-boring is done by many species of beetles, especially *Scolytidae*, which excavate characteristically formed branching passages tangentially in the inner bark of Conifers and other trees. Some of them also bore down to the surface of the sap wood *(e.g. Tomicus bidentatus)* or even burrow right into the latter *(e.g. T. lineatum)*. It commonly happens that the external apertures show up clearly, owing to the brown dust and excrement, sometimes accompanied by turpentine, which exude from them. Many of these Bark beetles only attack trees which are already injured by fire, lightning, etc.; possibly they cannot bore through a cortex which swamps them with sap, as a vigorous one might do.

Wood-boring is also done by many of the bark-beetles as well as by Longicorns, *e.g. Saperda* in

Poplars and Willows, the young shoots of which often show characteristic swellings with lateral holes indicating the points of exit. From the external apertures comminuted wood, like saw-dust, is frequently ejected in quantity and betrays the presence of the insects. Certain wood-wasps (*Sirex*) and the larvae of moths (*Cossus*) also make large perforations in the wood of Willows and other trees, often destroying it completely. In the case of these larger borers, whose tunnels may be as broad as the little finger, the foul smell as well as abundant "saw-dust" betray the evil.

Excavations in wood are by no means caused only by insects: several of the larger Hymenomycetes—*Stereum*, *Thelephora*, *Polyporus*, etc.—tunnel the timber in characteristic ways and often after a fashion very suggestive of insects. They usually obtain access through fractures.

Tunnels in leaves are invariably due to the activity of miners belonging to the smaller moths and beetles—*e.g.* *Tinea*, *Orchestes*, etc.—the larvae of which eat out the mesophyll but leave the covering epidermis or cuticle untouched, and since the insect bores forwards only, in an irregular track, and leaves its excrement in the winding passage, the effect is very characteristic.

Whitish leaf tunnels in Peas are excavated by *Phytomyza*.

Characteristic foxy-red tunnels are mined in the leaves of Apples by *Lyonettia*, *Coleophora*, etc.

Falling of fruit, of Apples, Plums, Apricots, etc., before they are ripe, is frequently due to insects, of

which the various species of *Grapholitha* or *Carpocapsa* are conspicuous: the fallen fruits show a small hole leading by a labyrinth of passages to the "core" or "stone," and in which the grub and its excrement are visible. The cuttting off of the vascular bundles and disturbance of the water supply only partly explain the premature fall.

Pith-flecks are minute brown specks or patches found in the wood-layers of many trees, and consist of dead parenchymatous thick-walled cells, reminding one of the structure of pith. They are explained as due to the borings of minute insects, *Diptera* or Beetles, the larvae of which pierce the cortex and phloem and bore their way into the cambium. The latter then occludes the tunnels by filling them up with cells, and continuing its wood-forming activity gradually buries them deeper and deeper in the wood. Such pith-flecks are common in Willow, Birch, Alder, *Sorbus*, etc. It is possible that they may be due to other causes also in other trees.

Erosions or *irregular wounds* on leaves are caused by large numbers of grubs and caterpillars and other insects, such as earwigs, as well as slugs, snails, and other animals; but it must by no means be assumed that all marginal leaf wounds, for instance, are caused by animals, since many fungi which rot the tissues, as explained below (p. 208), also cause such erosions, the putrescent parts falling out—*e.g.* the Potato disease.

Skeleton leaves frequently result from the

ravages of caterpillars, which leave the coarser ribs and veins untouched, but much finer skeletons with the minute veins almost intact may be found on plants infested with certain insects—*e.g. Selandria* on Cherries. Skeletonised patches on Cherry leaves, often pink or brown-pink, are eaten out by this grub.

Shot-holes are perforations in leaves presenting the appearance, from their more or less rounded shape, of gunshot wounds. They may be due to insects which bore through the young leaves while still folded in the bud—*e.g.* Willow Beetle —or which gnaw out the tissue—*e.g.* the Beech Miner. Similar but usually more torn and irregular holes are eaten out by many caterpillars—*e.g.* the Cabbage Moth.

Shot-holes on Peas may be the work of Thrips.

Leaf perforations are commonly caused by severe hail-storms, the hail-stones beating right through the thin mesophyll. Certain chemicals used for spraying have also been known to cause shot-holes by killing the tissue beneath the standing drops.

There is, however, a class of shot-holes in thin leaves which are due to the action of minute fungi, the mycelium of which so rots the tissues in a more or less circular area round the point of infection, that, in wet weather, the decomposing mass falls out and leaves a round hole—*e.g.* certain Chytridiaceae, Peronosporeae, *Glœosporium*, *Exoascus*, etc. If dry weather supervenes these holes frequently dry at the edges, and the leaves appear as if eaten out.

Shot-holes in Cherry, Walnut, Tobacco, and Plum leaves are due to *Phyllosticta*, in Cherry leaves also to *Clasterosporium*, and in Potato leaves to *Haltica*.

Frost-cracks.—The trunks of trees exposed to the north-east, and occasionally with other aspects, are apt to show longitudinal ridges which realise on a larger scale the features of healed wounds scored with a knife. These wounds are due to the outer layers of wood losing water from their cell-walls as it congeals to ice in their lumina, more rapidly than do the warmer internal parts of the trunk; as this drying of the wood causes its shrinkage, especially in the tangential direction, the effect of a sudden frost and north-east wind is to rend the wood, which splits longitudinally with a loud report, as may often be heard in severe winters. Since the cortex and bark are ruptured at the same time the total effect resembles that of a deep knife-cut, and the same healing processes result on a larger scale when the wood swells and closes up the wound again in spring. But this recently-closed lesion is evidently a plane of weakness, and if a similarly severe winter follows the wound reopens and again heals, and so on, until after a succession of years a prominent *Frost-ridge* results, which may finally heal completely if milder winters ensue or the tree be eventually protected.

Strangulations.—We are now in a position to understand the so-called strangulations which result when woody climbers, telegraph wires, etc.,

kill or injure trees by tightly winding round them. If strong wire is twisted horizontally round a stem, the growth in thickness of the latter causes the trapping of the cortex and cambium, etc., between the wire and the wood, and a ringing process is set up in consequence of the death of the compressed tissues. A callus then forms above the wound, as in the case of true ringing by means of a cut, and eventually bulges over the upper side of the wire: in the course of years this overgrowth may completely cover in the wire, and, pressing on to the lower lip of the wound, may at length fuse with the cambium below. Hereafter the thickening rings of wood are continuous over the buried wire. The process is obstructed by all the impediments referred to in dealing with ringing, and of course the stem thickens more above than below the wire. If the sapwood is thin, and the bark is so thick as to put great obstacles in the way of the junction of the upper and lower cambiums, death may result—the tree is permanently ringed. (See p. 201.)

Spiral grooves are frequently met with where Wood-bine or other woody climbers have twined round a young stem or branch, the upper lip of the groove always protruding more than the lower. If a kink or a crossing of two plants or branches of the twiner results in a complete horizontal ring, the results are as in the above cases of ringing and strangulation. Naturally grooved walking sticks are often seen.

Buried letters, etc.—These processes of healing by occlusion enable us to understand how letters of the alphabet, cut into the wood of trees, come to be buried deep in the timber as successive annual rings cover them in more and more. Chains, nails, rope, etc., have frequently been found thus buried in wood.

Notes to Chapter XXII.

In addition to the notes to the last chapter, the reader may be referred to Fisher in Vol. IV. of Schlich's *Manual of Forestry*, Chap. VI., for an account of Hess' excellent work on Boring Beetles, etc.

The authority on Wood-fungi is Hartig, see especially his *Zersetzungs-erscheinungen des Holzes*, the principal results of which are condensed in his *Diseases of Trees* already referred to. As regards "Pith-flecks," the reader should consult Frank, *Krankh. der Pflanzen*, B. I., p. 212: the subject needs further investigation.

CHAPTER XXIII.

EXCRESCENCES.

Herbaceous excrescences, or galls—Erineum—Intumescences—Corky warts, etc.—Pustules—Frost-blisters—Galls and Cecidia—Root nodules.

Excrescences, or out-growths of more or less abnormal character from the general surface of diseased organs, are very common symptoms, and widely recognised. They are due to hypertrophy of the tissues while the cells are young and capable of growth, and may be induced by a variety of causes, among which the stimulus of insect-punctures and of the presence of insect eggs are best known; but that of fungi, though less widely recognised, plays an equally important part, and, as we shall see, galls and other excrescences may be due to widely different agents.

Galls or *Cecidia* are protuberances of the most varied shapes, colours, and sizes found on herbaceous parts attacked by insects, fungi, etc. In the simplest cases the insects only pierce and

suck the young cellular tissue—*e.g. Phytoptus*, Aphides, etc.—but in others the stimulus to hypertrophy starts by the puncture of the embryonic tissue of a leaf, root, etc., by the ovipositor of the female insect, which then lays an egg—*e.g. Cynips*, *Cecidomyia*, etc.—the presence of which appears to intensify the irritating action, or such only occurs when the young larva escapes.

Our knowledge of the primary cause of gall-formation amounts to very little. Generally speaking, only embryonic or very young cellular tissue reacts, and galls on adult leaves and branches have usually been initiated long before. The same gall-insect may induce totally different galls on different plants, or even on different parts of the same plant, and different insects call forth different galls on any one plant. These facts point clearly to the co-operation of both plant and insect in the gall-formation, and the best hypothesis yet to hand is to the effect that a gall is a hypertrophy of cells, the normal nutrition, growth, and division of which have been disturbed owing to the action of some poison or other irritant derived from the insect, or fungus, or other organism. Attempts have been made to reproduce galls by injecting the juices of similar galls into the tissue, but as yet without success, and this may point to the co-operation of mechanical irritation during the hypertrophy in normal gall-formation.

Galls, in the broad sense, are not always preceded by a wound, however. Insects on the outside of young tissues may cause such irritations

that the parts in contact with the animal are arrested in their growth, while those further away grow more rapidly—*e.g.* where Mites, etc., cause puckers and leaf-rolling. In true galls the hypertrophy may consist merely in the enlargement of cells already present, and no new cell-divisions and, still less, changes in the nature of the tissues result—*e.g.* some pocket galls on *Viburnum*, *Pyrus*, etc., and the hairy outgrowths of the epidermis known as *Erineum*. In other cases there is not only hypertrophy of existing cells, but new cell-divisions are instituted : these cell-divisions may be confined to the direction perpendicular to the epidermis, and the tissues grow only in the direction of the surface, producing puckerings—*e.g.* the Aphis galls on *Ribes*, Phytoptus galls of *Salvia*, leaf galls on *Tilia*, *Acer*, *Alnus*, etc., and the curious galls on Plums due to *Cecidomyia Pruni*, and which must not be confounded with the "pocket plums" and similar galls due to Exoasci.

In a third series of cases, cell-divisions occur parallel to the surface of the leaf, and galls are formed which grow in thickness, and develop the most extraordinary and complicated new tissues —proteid-cells surrounding the egg or larva deposited inside, followed by a protective layer of sclerenchyma encasing this food layer, and around this again softer tissues which may assume the structures and functions of respiratory tissues, water-storing tissues, starch reservoirs, assimilatory, or protective tissues of various kinds,

and over all may be a well-marked epidermis, with stomata, or cork with lenticels.

The chief seat of these hypertrophies and—what is more remarkable—development of new tissue elements not found elsewhere in the leaves, or even in the species, is the mesophyll, and various speculations and hypothesis have been founded on these curious phenomena.

Erineum.—The simplest excrescences on plants are certain hair-like developments of epidermal cells due to the irritation of species of *Phytoptus*, and similar insects which rise in clusters on the surfaces of leaves and by their colours, consistence, arrangement in patches, spots, etc., so simulate fungi that Persoon was deceived by them and gave them the genus name *Erineum*. They occur on most of our trees, *e.g.* Poplar, Lime, Oak, and are very common in the Tropics. Usually pale or even white at first, they turn brown as the hair-like outgrowths die and lose their sap, but since the latter may be bright coloured—yellow, red, purple,—the patches are sometimes very conspicuous objects on smooth leaves.

In many cases these hairs exactly resemble in shape and other characters the abnormal root-hairs found on roots exposed to the effects of poisonous reagents, or of unsuitable food-materials, or the rhizoids developed from wounded Algae, etc.

Intumescences are similar trichomatous outgrowths not associated with insects or fungi, and due to some disturbance of the balance

between transpiratory and assimilatory functions of their leaves, as indicated by the less localised occurrence and by their non-appearance when the plant is under favourable cultural conditions. Structures not unlike these have been artificially induced by exposure to particular lights, and also by painting spots with dilute corrosive sublimate, indicating that poisons may impel the epidermis cells to grow out abnormally.

Corky warts.—Several forms of disease are known in which the pathological condition is expressed by the formation of cork in unwonted places and quantities. The *Scab* or *Scurf* of Potatoes is a case in point. The tissue of the lenticels absorbs water and the outermost cells are cut off by cork and die: the cells below them burst the dead bark-like masses thus formed, and again cork is formed and cuts off the outer masses, and the rough cork warts—*Scab* or *Scurf*—are the result.

The causes predisposing to scab have been variously assigned to dampness, want of lime, action of bacteria and fungi—*e.g. Sorosporium*, *Oospora*, *Spongospora*,—the latter making their way into the ruptured tissue of the lenticels and irritating the cells to further growth.

It seems probable that several different kinds of scab exist in Potatoes, as well as in roots—*e.g.* Beets, and the whole subject needs further investigation. The scab-like rough scaly bark of Pear trees in dry districts may also be mentioned here.

Cork-wings are well known on the young branches of Elms, Maples, etc., some varieties of which have received specific names on this account.

Corky excrescences on leaves occur occasionally in the Gooseberry, Holly and other plants, for which no cause has been discovered.

Lenticels are also formed on some leaf-galls, and are remarkable as being structures not normal on leaves.

Pustules.—This term may be employed generally for all slight upheavals of the surfaces of herbaceous organs, which subsequently burst and give egress to the spores, etc., of the organism causing them, or merely fray away at the top if no organism is discoverable. They are often due to fungi—*e.g. Synchytrium*, *Protomyces*, *Cystopus*, and Ustilagineae,—and we may extend the use of the general term also to those cases where the *stroma* of the fungus itself bursts through the cortex of older parts and forms the principal part of the pustule—*e.g. Monilia*, forming white or grey pustules on Apples, *Roestelia* and other Æcidia, forming yellow or orange pustules on leaves, etc.; *Cucurbitaria* and *Nectria* (red) breaking through the cortex of trees, and *Phoma* and numerous other Ascomycetes which form black cushions. *Pustules* on the leaves of *Lysimachia*, *Ajuga*, etc., are due to the parasitic Alga *Phyllobium*.

Cylindrical stem swellings are caused by *Calyptospora*: they are due to the hypertrophy of the cortex of Bilberry stems permeated by

the hyphae. *Epichloe*, which clothes the sheaths and halms of grasses with its stroma, at first snowy white and later ochre-yellow as the perithecia form, is another example.

The cylindrical layer of eggs of a moth such as *Bombyx* on a twig must not be confounded with these cases.

Frost-blisters are pustule-like uprisings of the cortex, where the living tissues below have formed a callus-like cushion into the cavity beneath the dead outer parts of the cortex which were killed by the frost ; they occur on the stems of young Apples, Pears, etc.

Galls in the narrower sense are tissue outgrowths usually involving deeper cell-layers. They are so varied and numerous that classification is difficult. For symptomatic purposes we may divide them as follows :

Leaf-galls.—A well-marked type is that of the *pocket-galls* or *bladders* in which the whole thickness of the leaf is as it were pushed up like a glove-finger at one spot, so that if the upper surface of the leaf forms the outside of the gall the lower surface is its lining. Such galls are common on Limes (*Phytoptus*), *Glechoma* (*Cecidomyia*), Elms (*Tetraneura*), etc. Similar localised extension of the leaf surface, compelling it to rise up like a pocket, are caused by fungi—*e.g. Taphrina* on Poplars, *Exoascus* on Birches, etc., *Exobasidium* on Bilberries, Rhododendrons, etc.

Another type is that of the *Gall-apple*, so well known on Oaks, where the spherical swelling is

solid—except for the inner cavity containing the eggs—*Neurotus*, *Cynips*, *Hormomyia*, etc. These are comparable in general characters to the nodules on roots.

Fungus galls with similar external features when young are found on Maize (*Ustilago Maydis*), and betray their nature by the black powdery spores as they mature.

Bud galls on Willows are due to *Cecidomyia*, which causes several internodes to swell out into a greenish barrel-shaped mass, from which leaves may spring.

Small irregular excrescences on Willow stems are referred to *Phytoptus*, and another species of the same insect induces similar swellings on Pines which are not surcharged with resin.

American Blight, or Woolly Aphis, on Apples especially, causes the tumour-like swellings covered with sticky white fluff, which is a waxy excretion of the insect. Galls on *Pilea*, in Java, are due to an Alga—*Phytophysa*.

Root-nodules or *nodosities* are frequently caused by insects—*e.g.* *Centhorhynchus*, a beetle which attacks Crucificers, *Cynips* and allied "gallflies" of Oaks, and the notorious *Phylloxera*. But similar root-galls are produced by Nematode worms, *Heterodora*, on Beets, Tomatoes, Cucumbers and numerous other plants, and by the Slime fungus *Plasmodiophora*, and it is not always easy to distinguish such cases from the fungus-galls (*Mycocecidia*) on the roots of Alders, *Juncus*, and Leguminoseae where the symbiosis of bacteria or fungi with

the roots are of benefit to the plant. *Urocystis Leimbachii* forms similar nodules at the collar of young plants of *Adonis*.

Heterodora javanica passes into the cortex of sugar-cane roots through fissures, and makes its way to the place where a young rootlet is about to emerge; here it sticks its beak into the growing-point and remains fixed.

Molliard has shown that in the roots of Melons, *Coleus*, etc., *Heterodora* causes the cells in immediate contact with its head, and which would normally become vessels of the xylem, to swell up into huge giant-cells, with their walls curiously folded, and containing large supplies of proteids and numerous nuclei, reminding us of the food-layer of insect galls and of the tapetal layer of pollen-sacs. While the stimulus exerted by the Nematode thus induces hypertrophy and storage with food-substances of these cells, those of the next layers undergo reticulate thickenings of their walls. Again instances of the evolution of new tissue elements by the action of the foreign organism.

So far as galls on leaves are concerned the amount and kind of damage done are in proportion to the area of chlorophyll action put out of play for the benefit of the plant, and the remarks already made on p. 193 apply here also. Where buds are destroyed the effects may of course extend further, but it rarely happens that leaf-galls are so abundant as to maim a tree permanently. Nevertheless we must remember that cases like *Phylloxera* are notorious.

Far more dangerous, however, are the root-galls due to such insects, because here the damage is not so local: the water-supplies are cut off, and injurious consequences result from the absorption of the products of decomposition in the soil.

Notes to Chapter XXIII.

In addition to the literature on galls quoted in the Notes to Chapter XIV., the reader should consult Dale "On certain Outgrowths (Intumescences) on the green parts of Hibiscus" *Proc. Cambr. Phil. Soc.*, Vol. X., 1899, p. 192, and *Brit. Ass. Rep.*, Bradford, 1900.

The detailed study of the anatomy and histology of Galls has been recently undertaken by Küster, "*Beitrage zur Kenntniss der Gallenanatomie*," Flora, B. 87, 1900, p. 117, where the principal references will be found.

On the root-galls due to Nematodes see Atkinson in *Science Contributions from the Agric. Expt. Station, Alabama*, Vol. I., p. 1, 1889; Percival, "An Eel-worm disease of Hops" in *Natural Science*, Vol. VI., 1895, p. 187; and Molliard in *Revue générale de Botanique*, Apl., 1900, p. 157, where the histology is dealt with.

The nodules of the roots of Leguminosae are not part of the subject of this work: the literature is collected in *Science Progress*, 1895, Vol. III., p. 252, and Dawson, *Phil. Trans.*, 1900.

CHAPTER XXIV.

EXCRESCENCES (*continued*).

Cankers—Burrs—Sphaeroblasts, and other excrescences of woody tissues—Witches' Brooms.

Cankers are irregular excrescences due to the perennial struggle between tissues attempting to heal up a wound, and some organism or other agent which keeps the lesion open. A canker always originates in a wound affecting the cambium, and usually in a small wound such as an insect puncture or frost nip; if undisturbed the dead parts would heal over by cork and callus, but if recurring frost-cracks break open the coverings, or if insects or fungi penetrate the callus and invade the cambium, irregularities of growth due to the occluding tissue on the one hand, and continued growth of the still unimpaired cambium on the opposite side of the injured shoot on the other, result in the canker. Frost cankers occur on fruit-trees, Vines, Beeches, etc.

Cankers due to insects are found on Apples, the cortex of which is punctured by the woolly Aphis (*Schizoneura*) while the twigs are young, and the wound is kept open by the insects nestling in crevices in the occlusion tissues. Species of *Coccus*, *Lachnus*, and *Chermes* also produce cankers on forest trees.

Cankers due to fungi usually originate in a wound primarily due to an insect puncture or bite, or to frost, the invading fungus hyphae making their way into the wounded tissues and gradually extending more and more into the cambium and the occluding callus. Among the best known of these wound fungi which cause cankers are *Dasyscypha Willkommii* the peziza of Larch disease, *Nectria ditissima* and *N. cucurbitula* on Beech and Conifers; less common are *Scleroderris* on Willows, *Aglaospora* on Oaks and some others.

Peridermium Pini and *Aecidium elatinum* also cause cankers under certain conditions, as also does *Gymnosporangium*, but in these cases the fungi are more truly parasitic.

In some cases—*e.g.* Ash, Pine, Olives—bacteria are concerned as associated organisms in the cankering of trees.

Burrs or *Knauers* are irregular excrescences, principally woody, with gnarled and warted surfaces. They are frequently due to some previous injury, such as the crushing or grazing of cortical tissues by cart-wheels. The excitation of the tissues thus wounded results in the development

of shoots from adventitious or dormant buds at the base of old tree trunks, or in the starting of the same process where a branch has been broken off. The new bud begins to develop a shoot, but soon dies at its tip owing to paucity of food-supplies to the weak shoot, while new buds at its base repeat the process next year with the same result, and each of these again in turn, and so on. The consequence is an extremely complex nest of buds, all capable of growing in thickness and putting on wood to some extent, but not of growing out in length. In course of time this mass may attain dimensions measurable by feet, forming huge rounded and extremely hard-knotted burrs, the cross-section of which shows the vascular tissues running irregularly in all directions, and, owing to the very slow growth, extremely dense and hard. The dark spots in such sections—*e.g.* Bird's-eye Maple—are the cut bud-axes all fused together, as it were. On old Elms such burrs are common at heights on the stem which preclude the assumption of any coarse mechanical injury, and similar structures occur on the boles of other forest trees suddenly exposed to light by the felling of their companions, which suggests that these epicormic shoots result from some disturbance due to the action of light.

Witches' Brooms are irregular tufts of twigs often found among the branches of trees such as Birches, Hornbeam, etc., where they look like crows' nests, and similar structures are to be found on Silver Firs and other conifers. In the former case they

are due to *Exoascus*, in the latter to *Aecidium*, fungi which are perennially parasitic in the shoots, and stimulate the twiggy development of a number of buds which would normally have remained in abeyance, or not have been formed at all, and only do so now in a fashion different from that of normal branches.

Rosette-like formations, depending on similar disturbing causes on the part of insects, occur in conifers—*e.g. Gastropacha Pini.*

Dense tufts of twiggy shoots may be developed on many trees by pruning in such a way as to stimulate the shooting out of basal buds which would otherwise remain dormant, *e.g.* Elm, Ash, and thus it occurs that injuries such as frost, insect bites, etc., may induce the production of such tufts in a tree crown. The dense nests of stool-shoots thrown up from felled tree-stumps are of essentially the same nature—partly adventitious and partly dormant buds being enabled to grow out because they can now be supplied with materials previously carried beyond them while the trunk was still there. Suckers, if repeatedly cut down, may also behave similarly.

Wood-nodules or *Sphaeroblasts* are curious marble-like masses of wood which protrude with a covering of bark from old trunks of Beeches, etc., and can be readily dug out with a knife. The nodule has arisen by the slow growth of the cambium of a dormant bud, the base of which separated at an early date from the wood beneath ; the cambium then closed in over the base and laid on

thickening rings all round the axis of the bud except at the extreme apex. When the separation occurred the cambium of the wood beneath covered over the previous point of junction, and thus the woody bud was pushed out with the bark, and now protrudes covered with a thin layer of the latter. Similar nodules are occasionally found on Apple trees.

Notes to Chapter XXIV.

For further information on Cankers the student should read Marshall Ward, *Timber and some of its Diseases*, Chapter X. Further, the discussion as to the causes of canker in Frank, *Krankheiten der Pflanzen*, B. I., p. 207, and B. III., pp. 167 and 172, and various papers in *Zeitschrift für Pflanzenkrankheiten*.

CHAPTER XXV.

EXUDATIONS AND ROTTING.

Tumescence—Rankness—Bursting of fruits, etc.—Root rot—Rot of fruits—Bulb diseases—Flux—Honey-dew—Slime flux—Resinosis—Gummosis—Manna.

I PUT together in one artificial class a varied group of diseases, the principal symptom of which is the escape of fluids from the tissues, under circumstances which betray an abnormal state of affairs, often obvious, but sometimes only to be inferred. In many of these cases bacteria abound in the putrefying mass, and some evidence exists for connecting these microbes causally with the disease in a few of the more thoroughly investigated cases, but in no case has this been sufficiently demonstrated; and considering the ease with which bacteria gain access *via* wounds caused by insects and fungi, as well as by other agents, the necessity for rigid proof must be insisted upon before we can accept such alleged examples of *Bacteriosis*.

Tumescence. — It occasionally happens that herbaceous parts of plants pass into a condition of over-turgescence from excess of water in the tissues, an abnormal state which indicates pathological changes resulting from various causes, often not evident and therefore regarded as internal. Such disease was formerly termed *Œdema* or *Dropsy*. This disease is frequently due to the excessive watering of pot plants with large root systems and deficient foliage, in hot-houses with a saturated atmosphere: it is, therefore, primarily referable to diminished transpiration. It can sometimes be brought about by covering potato plants, for instance, with a bell-jar in moist, hot weather; and this, and the prevalence of the disease in hot-houses as compared with plants grown out of doors, point to the above explanation. Similar phenomena do occasionally occur out of doors in hot, moist situations or during wet seasons, however, and the watery shoots of rank vegetation are merely particular cases of the same class. Moreover, the well-known tendency to succulence of sea-side varieties of plants which have thin herbaceous leaves when growing inland, points to the action of the environment in these matters, excess of salts being no doubt one factor in such cases.

Rankness affords another example where superfluity of water is concerned, though it does not involve simply this, because the plant may also contain excessive quantities of nitrogenous and mineral matters taken up by the roots.

Rankness is, in fact, in many respects analogous to etiolation in so far as the tissues are soft and surcharged with water, but it differs fundamentally in the deep green of the chlorophyll: this may lead to abundant assimilation if free access of air and drier conditions can be gradually brought about. Any sudden drying, however, may be fatal to the tender tissues.

Rankness commonly depends on excess of food materials, especially nitrogenous manures, as may be seen in meadows and cornfields where the manure heaps have remained on the ground and saturated it to excess as compared with the rest of the soil; this may often be observed with weeds, etc., in the neighbourhood of farm-buildings. If the period of rank growth is accompanied and followed by days of suitably bright sunshine and dry air, the increase of vegetative structures usually results in increased flowering, heavy crops, or strong wood; but if the rankness continues too long, or is accompanied by wet and dull weather, the watery tissues are peculiarly susceptible to attacks of fungi and insects, and to damage by sudden frosts or chilly winds. Rankness affords, in fact, a typical illustration of predisposition to disease.

Damping off.—When seedlings are too closely crowded in beds kept too damp, or in moist weather, they are very apt to rot away, with all the symptoms—spreading from a centre, contagious infection, mycelia on and in the tissues, etc.—of a fungus attack. The commonest agent

concerned is one of the species of *Pythium*, the propagation of which is favoured by the rank, over-turgid, and etiolated conditions of the plants. Species of *Mucor*, *Botrytis*, and other fungi, may also be met with.

Bursting of fleshy fruits, such as Tomatoes, Grapes, etc., is due to over-turgescence in rainy weather or excessively moist air. But the phenomenon is by no means confined to such organs. Hot-house plants when oedematous not infrequently put out watery blisters from the cortex or leaves, which rupture; and the stems of fleshy fasciated (*e.g.* Asparagus) or blanched and forced plants (*e.g.* Celery, Rhubarb) are particularly apt to crack here and there from the pressure of the turgescent tissues on the strained epidermis. Beets, Turnips, and other fleshy roots show the same phenomena in wet seasons. That these ruptures and exposures of watery tissues afford dangerous points of entry for parasites and moulds will be obvious—*e.g.* *Edelfäule*, a rotten condition of the grapes in the Moselle district.

Root-rot is a common disease in damp, sour clay soils after a continuance of wet weather—*e.g.* Wheat, especially if root-drawn and exposed to thaw water.

In the disease known as Beet-rot, the roots turn black at the tip, where the tissues shrivel and become grooved and wrinkled extensively. Inside the flesh also blackens and finally rots. In earlier stages, only the vascular bundles are brown and blocked with gum-like substances.

In advanced stages there is much gummy material in the lumina, and even large cavities filled with this gum may be found.

The rot of Cherries, Pears, Apples, Plums, etc., in store may be due to several fungi, of which *Botrytis*, *Monilia*, *Mucor*, *Penicillium*, and *Aspergillus* are the chief. The fruit may be attacked while still on the tree, but very often fungi and bacteria gain access to the tissues, through bruises, cracks, etc., formed in the fruit lying in the storage baskets or on the shelves.

Rot in Onions, Hyacinth bulbs, etc., is frequently due to the access of *Botrytis* or *Sclerotinia*, followed by moulds, yeasts, and bacteria in the stores.

Sour-rot in Grapes, and other fleshy fruits which need much sun to ripen them, is probably a usual result of continued cold, wet weather at the cropping season, setting in when the fruits are beginning to swell.

Flux.—It is a common event to see fluids of various kinds issuing from wounds in trees, or congealing in more or less solid masses about them; and owing to the prevailing tendency to compare plant diseases with those of animals, we find such expressions as *Gangrene*, *Ulcer*, and so forth, applied to these "open sores." In so far as such outflowings frequently indicate diseased states of injured tissues which are incapable of healing up, the analogy is perhaps a true one; but it must be remembered that very different structures and processes in detail are concerned. Moreover,

liquid excretions more or less indicative of diseased states are by no means confined to wounds or definitely injured tissues, in which case such terms are wholly misapplied.

Honey-dew.—The leaves, or other organs, of many plants are sticky in hot weather, owing to the excretion of a sweet liquid containing sugar, the consistency and colour of which vary according to circumstances. This honey-dew must not be confounded with the normal viscidity of certain insectivorous plants—*e.g.* Sundew—or with the sticky secretion on the internodes of species of *Lychnis*, etc., where it plays the part of a protection against minute creeping things.

Honey-dew is often met with on Lime trees, Roses, Hops, etc. In many of these cases the honey-dew is excreted by Aphides, which suck the juices of the leaves and pour out the saccharine liquid from their bodies. The sweet fluid is in its turn sought after by ants, and also serves as nutritive material for various epiphytic fungi—*e.g.* sooty mould, *Capnodium*, *Fumago*, and *Antennaria*—which give the leaves and honey-dew a brown or black colour. Certain *Coccideae* also excrete honey-dew, especially in the tropics.

At least one case is known where honey-dew is formed as the result of the parasitic action of a fungus, namely *Claviceps purpurea* in its conidial stage on the stigmas of cereals, and this may be compared with the sweet odorous fluid excreted by the spermogonia of certain *Aecidia*. In both

cases the sweet fluid attracts insects which disperse the spores.

Honey-dew may also be formed without the agency of fungi or insects, when hot and dry days are followed by cool nights, with a saturated atmosphere, *e.g. Caesalpinia*, *Calliandra* and other trees in the tropics, which are called rain trees owing to the numerous drops of fluid which drip from the leaves under the abnormally turgescent conditions referred to.

Cuckoo-spit.—The leaves of Willows, Meadow grasses and herbs, etc., are often seen with froth on them, in which is a green insect, *Aphrophora*, which sucks the juices from the tissues and excretes the frothy watery cuckoo-spit from its body.

Slime-flux.—The trunks of trees may sometimes be observed to pour out a slimy fluid from cracks in the bark, or from old wounds, or branch scars. In some cases, *e.g.* in Oaks, the slime has a beery odour and white colour, and abounds in yeasts and other fungi to the fermentative activity of which the odour and frothiness are due. In other cases the slime is red *e.g.*—Hornbeam; or brown—*e.g.* Apple and Elm; or black—*e.g.* Beech, the colour in such cases being due to the mixture of yeasts, bacteria, and fungi with which these slimes abound. The phenomenon appears to be due to the exudation of large quantities of sap under pressure—root pressure—and is primarily a normal phenomenon comparable to the bleeding of cut trees in spring: the fungi, etc., are doubtless

saprophytes, but their activity is concerned with the putrefactive processes going on in the diseased wood, and which may lead to rotting of the timber.

The origin of the wounds in the bark and cortex, and which extend into the wood and other tissues as the putrefactive and fermentative processes increase, appears to be in some cases at least due to lightning.

Resin-flux or *Resinosis.*—The stems of Pines and other conifers are apt to exude resin from any cut or wound made by insects, or by the gnawing of other animals; but in many cases the flow is due to fungi, *e.g. Peridermium*, the hyphae of which invade the medullary rays and resin canals and thus open the way to an outflow through cracks in the bark. *Agaricus melleus* not only invades the resin passages, but stimulates the tree to produce abnormal quantities of resin, which flows down to the collar and roots, and exudes in great abundance at the surface of the soil. Various other plants also exude resin from wounds, and in some cases the flux seems to be increased by degeneration of the tissues, *e.g. Copaifera.*

Gummosis.—Cherries, Apricots, Acacias, and many other trees are apt to produce abnormal quantities of gum, which flows from any wound or exudes through cracks in the bark. Degeneration of the wood-cells, and especially of the cell-walls of a soft wood formed by abnormal activity of the cambium, points to its origin being due, in some

cases at any rate, to a conversion of the cellulose, and fungi are sometimes found in the masses of gum; but beyond the fact that *gummosis* is a pathological phenomenon we know very little of the disease.

With regard to such gumming, it is significant how frequently pruned trees—Cherries, Oranges, Lemons, Plums, etc.—suffer.

Manna flux.—Certain trees, such as the Manna Ash, species of Tamarisk, etc., yield manna from wounds, and in some cases the latter are due to insects, *e.g. Cicada.*

The Potato-disease is best known by the pale whitish fringe, giving an almost mealy appearance to the margins of the brown to black patches in damp weather. In dry weather the brown patches shrivel and dry, and as they are apt to be at the edges and tips of the leaflets, these curl up. The young disease spots are yellowish, and the leaves of badly affected plants are apt to be sickly yellow throughout.

This Potato-disease due to *Phytophthora* must be distinguished from the curling and puckering, with wilting and browning of the leaves and yellow glassy look of the stems, due to the invasion of the vessels by a fungus which lurks in the tubers, and gains access thence to the shoots.

In the disease traceable to *Phytophthora* the stock remains green and the leaves plump and plane, and only the brown patches slough out in wet or shrivel in dry weather, and are bordered by the pale whitish zone of conidiophores.

In the leaf-curl the yellow and flaccid appearance of all the leaves of a stalk, or even of the plant, is the striking symptom, and the stem soon droops and blackens just above the soil, a white mould appearing also at the black spots. Subsequently black spots appear higher up, and bacteria gain an entrance. The stolons rot, and eventually the roots and the leaves wither. The tubers appear sound, but are small; they are apt to rot in the store, the vascular zones turning brown.

This leaf-curl has been ascribed to *Pleospora*, *Polydesmus*, *Verticillium*, and other parasites, as well as to excessive manuring and other agencies, but it still needs explanation.

Rot of Potato tubers in the soil, or in store, may be brought about by very different agents.

If *Phytophthora* has obtained access, the fungus hyphae spread between the cells, starting from the haulm, and cause the flesh to turn yellowish and then brown in patches. On the exterior are discoloured patches, depressed, with the flesh beneath brown and soft. The mycelium spreads mostly in the outer layers, which though they turn deep brown remain firm.

Wet rot of potatoes may be due to various fungi, and, in excess of water, to putrefactive bacteria (*e.g. Clostridium*), which destroy the cell-walls. The flesh becomes soft, then soup-like, and finally putrefies to a liquid mass with a vile smell of butyric acid, etc., in which the starch grains may be seen floating.

Tubers are often found with the cork burst and

peeling in shreds, the flesh more or less converted into a putrid and stinking pulp, with a spotted brown boundary of partly destroyed but firmer tissue between the dark utterly rotten and the white and still firm healthy flesh. The principal agent in the destruction of the tissues is *Clostridium*, an anaerobic bacillus which consumes the cell-walls but leaves the starch intact. Hence a thoroughly decomposed tuber consists of a cork bag full of starch and foetid liquid. In the dried condition the flesh shows a brown marbling ; this passes into a soft soupy starchy part, and here and there may be violet grey cavities lined with *Spicaria*, *Hypomyces*, etc., the white stromata of the latter often appearing externally. The excavations are filled with loose starch grains, and bounded by cork and cambium formed in the peripheral cells. The cell-walls eventually undergo slimy decomposition.

Spicaria, *Fusisporium*, various moulds, and bacteria may all be associated with wet-rot.

Dry-rot of Potatoes is also due to various fungi and bacteria, but the destructive action goes on slowly, owing to there being no more moisture than the tissues afford. The flesh becomes excavated here and there, owing to the slow destruction of the cell-walls by *Clostridium* : the destroyed tissues are brown, and the uninjured starch grains powder them all over. Finally the whole shrunken mass has a crumbly consistency.

When the flesh remains white, but assumes a powdery consistency and dry-rot, with the cork

destroyed here and there, Frank refers the damage to *Phellomyces*. Where the dry-rot is due to *Fusarium* the chalk-white stromata may often be detected breaking through the periderm; but it must be remembered that the soil-contaminated, broken skin of a potato-tuber is a favourable lurking spot for many fungi, and *Periola*, *Acrostalagmus*, and others have been detected therein.

Brown spots, depressed into the flesh, sometimes result from the ravages of *Tylenchus*, the minute worms being found in the diseased tissues.

In some cases the flesh turns watery and soft, grey, almost glass-like, starting at the haulm end, and this may be owing to the invasion of *Rhizoctonia*.

Notes to Chapter XXV.

The rotting of bulbs, roots, etc., has been much discussed during the last few years in the pages of the *Gardeners' Chronicle*, *Zeitschrift für Pflanzenkh.*, and elsewhere. The principal references to Bacteriosis—the rot in which bacteria are stated to be the primary agent causing these and similar diseases—may be found in Massee, *Diseases of Plants*, pp. 338-342, and more fully in Russell, *Bacteria in their Relation to Vegetable Tissue*, Baltimore, 1892; and in Migula, *Kritische Uebersicht derjenigen Pflanzen-krankheiten, welche Angeblich durch Bakterien verursacht werden*, Semarang, 1892.

The most convincing accounts, however, are since that date; see Smith, "Pseudomonas Campestris," *Cent. f. Bakt.*, B. III., 1897, p. 284, and Arthur and Bolley, *Bacteriosis of Carnations*, Ferdue University Agr. Expt. Station, 1896, Vol. VII., p. 17. Woods has lately shown that this disease is due to Aphides only, the bacteria having nothing to do with the disease primarily, *Stigmonose*, *Bull.* 19, U.S. Dept.

Agr., 1900; but it is necessary to bear in mind that actual penetration of the cell-walls from without must be proved, as De Bary proved it for germ-tubes of fungi, before the evidence that Bacteria are truly parasitic in living plants can be called decisive. This is a difficult matter, but until it is settled we do not know whether these organisms are really parasitic in the sense that *Phytophthora* is, or merely gain access by other means—I have traced them through dead fungus-hyphae—to the vessels, dead cell-walls, etc. The proof of infection *via* water pores and vessels is given for one species by Harding, "Die Schwarze Faulnis der Kohls," etc., *Cent. f. Bakt.*, Abh. II., B. VI., 1900, p. 305, with literature.

Concerning the "Damping off" of seedlings, see Marshall Ward, "Observations on the Genus Pythium," *Quart. Journ. Microsc. Soc.*, Vol. XXIII., 1883, p. 485, and Atkinson, *Bull.* 94 *of Cornell University Agric. Expt. Station*, 1895, p. 233.

On Bacteriosis in Turnips, see Potter, *Proc. R. S.* 1901, Vol. LXVII., p. 442.

CHAPTER XXVI.

NECROTIC DISEASES.

Patches—Frost-patches—Bruising due to hail, shot, etc.—Fire—Sun-burn or scorching—Sun-cracks. Dying-back—Frost—Fungi—Wound fungi—Defoliation by insects—Defoliation by hand—Stagshead.

Necrosis.—This is a general term for cases where the tissues gradually turn brown or black in patches which die and dry up, the dead area sometimes spreading slowly and invading the usually sharply demarcated healthy tissues around. It is a common phenomenon on the more slender stems or branches of trees, especially those with a thin cortex, and the terms *Brand* or *Scorching* sometimes applied signify the recognised resemblance between burnt patches and these dead areas of necrotic tissue.

Necrosis is often due to frost, which kills the cortex of Pears, Beech, etc., in patches of this kind. The dead cortex and cambium stick to the wood beneath and contract as they dry. The living

cambium and cortex around them then begin to push in callus towards the centre of the necrotic area; but since this callus is formed under the pressure of the cortical tissues it does not form a thick lip or margin to the healing wound, as it does in a Canker, but insinuates itself with thinned-off edges between the wood and the dead tissue, or at most traps a little of the latter in the final closing up of the wound. It is easy to see how such an area of Necrosis may become a Canker if the dead tissues split or slough off, and fungi or insects obtain access to the callus at the margins of the area, setting up the disturbances described on p. 222. As matter of fact many Cankers—*e.g.* those of the Larch disease, and those due to *Nectria*, or Aphides, etc.—often begin as flattened or depressed areas of Necrosis started by frost, and many small necrotic patches would eventually become Cankers if not healed up by the callus.

Necrosis may also be due to the bruising of the tissues by large hailstones, to gun-shot wounds, or to any form of contusion which kills the living cells of cortex and cambium.

Necrosis is a natural and common result of fire, and it frequently happens after forest-fires which have run rapidly through the dry underwood, fanned by steady winds, that the lower parts of the boles are scorched on one side only. The killed cambium and cortex then dry up in black necrotic patches, which may eventually heal up by intrusion of callus from the uninjured parts.

Sun-burn or *Scorching*.—If thin-barked trees,

such as Hornbeam, Beech, Firs, etc., which have been growing in partial shade owing to dense planting, are suddenly isolated by thinning, the impingement of the sun's rays on the south-west side during the hottest part of summer days may kill the cambium, and produce necrosis of the cortical tissues, and such necrotic patches heal very slowly or not at all, because the dead tissues have contracted so tightly on to the wood below that the callus cannot readily creep between.

Sun-cracks are due to intense insolation on the south side of trees in clear weather in early spring, causing the drying and contraction of the wood and its coverings down that side of the tree: the contracted tissues consequently split, as in the case of frost-cracks, the healing up of which is very similar.

Dying-back.—All that is true of the necrosis of cortical tissues in small patches also applies to cases where the whole of the outer tissues of thin twigs and branches die of inanition owing to a premature fall of leaves—*e.g.* after a severe attack of some insect or fungus pest. The consequent arrest of the transpiration current and the proper supply of nutriment to the cambium and cortex explain the phenomena. The younger branches of Coffee trees suffering from severe attacks of leaf-disease are often denuded of leaves and die back from the causes mentioned, the whole of the outer tissues becoming necrotic, and drying up tight on to the wood, because other branches with functionally active leaves on them divert the

transpiration current, and drought and inanition supervene.

Dying-back is frequently also a direct effect of early frosts, which kill the thin twigs before the "wood is ripened," as gardeners say.

Dying-back is also a frequent result of direct frost action on thin watery shoots or "unripe wood," and is apt to occur every year in certain varieties of Roses, for instance, in particular situations, such as "frost-beds," or aspects exposed to cutting winds, and so forth. The necrosis which results may affect all the tissues, or only the cortex and cambium, and the frequent accompaniment of all kinds of saprophytic *Ascomycetes* and moulds or other fungi is in no way causal to the phenomenon.

Dying-back may also be caused by fungi, and not necessarily parasites, for cases are often observed where saprophytes only are to be found in the necrotic tissues of the cortex, having made their way in through minute cracks, lenticels, etc.

A simple case is often seen in Chrysanthemums, Roses, etc., chilled and wetted to danger point, but not frozen, during the nights of autumn. The lowered resistance of the chilled tissues enables fungi like *Botrytis cinerea* to gain a hold, and the peduncles die-back with all the symptoms of Necrosis, the fungus gaining power more and more as its myceliun spreads in the dead tissues.

Many other cases are known where wound-fungi, such as *Nectria*, *Cucurbitaria*, *Phoma*, etc., in themselves incapable of true parasitism, gain a hold

on the necrotic tissue of a wounded twig, and having laboriously accumulated a vigorous mycelium saprophytically, extend into other parts. In many of these cases the dying-back of the twigs is expedited owing to the mycelium invading the medullary rays and wood vessels, and so obstructing the transpiration current. The much more rapid spread of the hyphae up into the parts thus killed sufficiently indicates the fundamentally saprophytic character of such fungi.

Dying-back in all its forms is a common result of defoliation by insects, *e.g.* caterpillars, especially if it occurs when the wood is depleted of reserve materials, and thus cannot supply the auxiliary buds and enable the twigs to clothe themselves with a new flush of foliage, a common danger in Conifers.

Any form of defoliation—*e.g.* excessive plucking of tea and mulberry leaves, browsing of animals, etc.—exposes the twigs to the dangers of dying-back, the accessory phenomena being similar to those already described.

Stag-head.—Old trees, though vigorous and in full foliage throughout the crown generally, frequently lose the power of bearing leaves on their topmost branches and twigs, which stand out bare and brown, and fancifully resemble the antlers of a stag: hence the forester's name "stag-head." This "top-dry" condition is frequently due to the removal of litter, or to excessive draining, or to the roots having gradually penetrated into unsuitable soil. The consequence is that some dry summer

the drought causes the breakage of the water columns above, and the twigs die back.

Tropical trees may also become *stag-headed* owing to the attacks of *Loranthus* and other parasites, the portions above the point of attachment dying back from inanition.

Cases also occur in the tropics where the *stag-head* condition is due to the persistent roosting of frugiferous bats—"flying foxes"—which tear the bark and foliage with their claws, and befoul the twigs generally.

Notes to Chapter XXVI.

The principal literature as regards frost is given in the works of Frank, Sorauer, and Hartig already referred to. An excellent summary will be found in Hartig's *Diseases of Trees*, p. 282, and in Fisher "Forest Protection," Vol. IV. or Schlich's *Manual*, p. 423.

CHAPTER XXVII.

MONSTROSITIES AND MALFORMATIONS.

Monstrosities—Teratology—Atrophy of organs—Shanking of grapes—Barren fruit trees—Dwarfing—Distortions and malformations — Fasciations — Flattened roots—Torsions—Curling and puckering —Leaf rolling -So-called "spontaneous" teratological changes.

Monstrosities.—In a wide sense this term is applicable to many cases here treated under other headings, and signifies any departure from the normal standard of size, form, arrangement, or number of parts, and so forth, due to arrest of growth, excessive growth of parts, or of the whole organs, etc.

Such *teratological* conditions are however by no means always *pathological*: that is to say, they may be variations which do not threaten the existence of the plant. In some cases they are clearly due to exuberant nutrition, and although they may occasionally predispose to disease, in

others they show no evidence of doing so. The whole practice of horticulture and agriculture abounds in examples of teratological sports or varieties which are transmissible by seeds, budding and grafting, and other means—*e.g.* double flowers, hypertrophied floral organs (cauliflowers), seedless grapes and oranges, crested ferns, etc.; and even when such varieties could not live as such in a state of nature, there is evidence to show that many of them readily revert to the original seed-bearing or single condition, and adapt themselves to the altered environment.

Every part of the plant may exhibit teratological changes, and I shall for the most part select cases in illustration which indicate approach to pathological states, and group with them cases known to be pathological in origin.

Atrophy is a common phenomenon denoting dwindling or reductions in size of organs due to insufficient nutrition, or arrest of growth from various causes.

Atrophy of leaves is a common result of the attacks of parasitic fungi, even when the latter induce local hypertrophy—*i.e.* excessive growth of particular parts, *e.g. Synchytrium* on Dandelions and Anemones. *Puccinia suaveolens* causes partial atrophy of the leaves of Thistles, *Aecidium Euphorbiae* of those of *Euphorbia.*

The carpels of Anemone are atrophied in plants attacked by *Aecidium*, and the whole flower is suppressed in Cherries infested with *Exoascus Cerasi*, while other fungi—*e.g. Cystopus*, *Exoasci*,

etc.—cause atrophy of the seeds, and numerous instances of atrophied grain occur in plants infested with Ustilagineae.

Atrophy of the grains of cereals is sometimes due to the direct attack of animals, *e.g.* eel-worms (*Tylenchus*) eat out the grains of Corn; weevils and other beetles (*Curculio*, *Bruchus*, etc.) similarly devour the contents of grain and nuts, the flowers of Peas and Apples, and so forth, inducing atrophy of the parts left. Still more striking cases are afforded by small insects which bore into the halms of cereals, and cause atrophy of the whole ear—*e.g.* *Cephus* in Wheat and Rye. Barley occasionally withers after flowering, the grain atrophying from no known cause, terms like *consumption* given to the disease conveying no information.

Atrophy of young fruits is commonly due to the flowers not setting—*i.e.* some agent has interfered with the normal transference of the pollen to the stigma. This may be due to excessive rain washing out the pollen (*e.g.* Vine), to a lack of the necessary insects which effect pollination, often seen in greenhouse plants; to the stamens being barren—*e.g.* certain varieties of Vine—or to the premature destruction of the stigmas by frost, as in Cherries, Pears, etc., or by insects, as in Apples, or fungi, *e.g.* the infection of bilberries with *Sclerotinia*; or even by poisonous gases, as is sometimes seen in Wheat, etc., growing near alkali works. Drought is also a common cause of atrophy of young Plums.

Shanking of Grapes is a particular case of atrophy and drooping of the immature fruits, due to the supplies being cut off by some agency. It may arise from very various causes which bring about disease in the leaves or roots, and should always be looked upon as a sign of weakness in the Vine, the structure of which is affected, *e.g.* poor wood—or the functions interfered with, *e.g.* water supplies deficient owing to paucity of roots.

Barren Apple, Pear, Plum, and other flowers are often found to have been bored through the petals while in bud, and the whole "heart" of the flower eaten out by the grubs of *Anthonomus*, leaving the unopened buds brown and dead, as if killed by frost or drought, and often erroneously supposed to be so.

The wilting and shrivelling of Clover is sometimes due to *Sclerotinia*, the mycelium of which pervades the roots and stock, on which the sclerotia may be found. Lucerne is similarly killed in Europe by the barren mycelium of *Leptosphaeria*, which may be found as a purple mat on the roots.

Dwarfing consists in partial atrophy of all the organs, and is a common result of starvation in poor, dry, shallow soils, as may often be seen in the case of weeds on walls or in stony places. Dwarfs which are thus developed in consequence of perennial drought are not, however, necessarily diseased, in the more specific sense of the word; their organs are reduced in size proportionally

throughout in adaptation to the conditions, and simply carry out their functions on a smaller scale.

Dwarfing is frequently a consequence of the lack of food materials, or of some particular ingredient in the soil, and in such cases is a diseased condition of some danger; similar results may ensue in soils containing the necessary chemical elements, but in unavailable forms.

Dwarfing may also be brought about by repeated maiming, nipping off the buds, pruning, etc., as in the miniature trees of the Japanese; and the case of trees continually browsed down by cattle, or of moor plants perennially dwarfed by cutting winds, are further illustrations in the same category, as are also those of certain alpine and moraine plants, whose only chance of survival depends on their adapting themselves to the repeated prunings suffered by every young shoot which rises into the cutting winds, since there is no question of lack of food-materials in these cases.

The practice of the Japanese is to pinch out the growing tips of the shoots wherever they wish to prune back, and it is by the judicious use of this heading in, and suitable pot-culture, that the dwarfs are made, 6-20 inches high at from 30-80 years old.

Dwarfing is often brought about by grafting on a slow-growing stock, and this method is employed in practice, as are also heading in, pruning of roots, and confinement in pots.

Dwarfing may also be due to poor or shrivelled —partially atrophied—seeds or such as have had their endosperms or embryos injured by insects or fungi, and although it is possible to nurse such dwarfs into normal and vigorous plants with good culture, they do not usually recover under natural conditions in competition with more vigorous plants.

Distortions or *Malformations* may be defined as abnormalities in the form of organs which concern all, or nearly all the parts, and do not refer merely to swellings or excrescences on them or excavations, etc., in them.

Fasciation.—Shoots of Asparagus, Pine, Ash, and many other plants are occasionally expanded into broad ribbon-like structures often studded with more than the normal number of buds or leaves, etc., such as would be found on the usual cylindrical shoots. Such *fasciations* are due to several buds fusing laterally under compression when young and the whole mass growing up in common, or, in a few cases, to the unilateral overgrowth of one side of the terminal bud. Fasciations appear to depend on excessive nutrition in rich soils. They may spread out above in a fan-like manner, exaggerating the abnormality, or they may revert to the original form. Some cases are more or less fixed by heredity—*e.g. Celosia.* Fasciated stems are frequently curved like a crozier, owing to one edge growing more rapidly than the other.

Cauliflowers are really cultivated monstrosities.

Fasciated Dandelions, *Crepis*, monstrous Chrysanthemums, peloric *Linaria*, five-leaved Clovers, spiral Teazels, etc., may all, if grown with care, be kept more or less constant in the monstrous state. That is to say, the particular kinds of variation here manifested can be maintained in proportion as the external conditions controlling the variation are maintained. Such conditions are chiefly rich supplies of food-stuffs, plenty of water and air, suitable temperature and lighting, etc. Mutilations, favouring the development of abnormal buds may also induce fasciations.

Torsions or spiral twistings of stems also frequently arise among plants grown in rich soils, and are often combined with fasciations—*e.g.* Asparagus, *Dipsacus*; and De Vries has shown that the peculiarity is not only transmissible by seed, but may be more or less fixed by appropriate culture.

Contortions of stems are often due to the unequal growth on different sides of the stems owing to the presence of fungi—*e.g.* *Cæoma* on Pines, *Aecidium* on Nettles, also *Puccinia* on petioles of Mallow, *Cystopus* on inflorescences of *Capsella*, etc.

Distortions of roots may be brought about in various ways by the hindrances afforded by stones.

Spiral roots occur occasionally in pot plants.

Flattened roots usually result from compression between rocks, the young root having penetrated into a crevice, and been compelled to adapt itself later. The distortions of stems by constricting

climbers, wire, etc., have been described, and fruits—*e.g.* Gourds—are easily distorted by means of string tied round them when young.

Distortions of leaves are very common, and are sometimes teratological—*i.e.* due to no known cause—*e.g.* the pitcher-like or hood-like *cucullate* leaves of the Lime, Cabbage, *Pelargonium*, etc., and of fused pairs in *Crassula*. Also coherent, bifurcate, crested, displaced and twisted leaves occasionally met with, and in some cases fixed by cultivation, may be placed in this category.

Puckers must be distinguished from pustules, since they consist in local upraisings of the whole tissue, not swellings—*e.g.* the yellowish green pockets on Walnut leaves, due to *Phyllereum*.

Puckered leaves in which the area of mesophyll between the venation is increased by rising up in an arched or dome-like manner are sometimes brought about by excessive moisture in a confined space.

Leaf-curl is a similar deformation caused by fungi, such as *Exoascus* on Peaches.

Wrinkling or puckering of leaves is also a common symptom of the work of Aphides—*e.g.* Hops.

Characteristic curling and puckering, with yellow and orange tints, of the terminal leaves of Apples, Pears, etc., are due to insects of the genera *Aphis*, *Psylla*, etc.

Small red and yellow spots with puckerings and curlings of the young leaves of Pears, the spots turning darker later on, are due to *Phytoptus*.

Leaf-rolling.—The leaves of Beeches, Poplars, Limes, and many other plants, instead of opening out flat, are often rolled in from the margins, or from the apex, by various species of *Phytoptus*, *Cecidomyia*, or other insects, which puncture or irritate the epidermis in the young stages and so arrest its expansion in proportion to the other tissues. According as the lower or upper surface is attacked the rolling is from the morphologically upper surface downwards, or *vice versa*. Very often the mesophyll is somewhat thickened where rolled and *Erineum*-like hairs may be developed—*e.g.* Lime. Many caterpillars also roll leaves, drawing the margins inward to form shelters—*e.g.* *Tortrix viridana*, the Oak leaf-roller. Certain beetles—*Rhynchitis*—also roll up several leaves to form a shelter in which the eggs are laid.

Webs are formed among the mutilated leaves of Apples by the caterpillars of *Hyponomeuta*.

It must be borne in mind that instances can be found of teratological change of every organ in the plant—*e.g.* stamens transformed into carpels or into petals ; anthers partly polliniferous and partly ovuliferous ; ovules producing pollen in their interior, and so on, being simply a few startling examples of what may happen. Such abnormalities are frequently regarded as evidence of internal causes of disease, and this may be true in given cases ; in a number of cases investigated, however, it has been shown that external agents of very definite nature bring about just such deformations as those sometimes cited as examples of teratology

due to internal causes, and the question is at least an open one whether many other cases will not also fall into this category. The study of galls has shown that insects can induce the formation of not only very extraordinary outgrowths of tissues and organs already in existence, but even of new formations and of tissue elements not found elsewhere in the plant or even in its allies; and Solms' investigations on *Ustilago Treubii* show that fungi can do the same, and even compel new tissues, which the stimulating effects of the hyphae have driven the plant to develop, to take part in raising and distributing the spores of the fungus —*i.e.* to assume functions for the benefit of the parasite. Molliard has given instances of mites whose irritating presence in flowers causes them to undergo teratological deformations, and Peyritsch has shown that the presence of mites in flowers induces transformations of petals into sepals, stamens into petals. Similarly De Bary, Molliard, Magnus, Mangin, and Giard have given numerous cases of the transformation of floral organs one into another under the irritating action of fungi, of which the transformation of normally unisexual (female) flowers into hermaphrodite ones, by the production of stamens not otherwise found there, are among the most remarkable.

These and similar examples suffice to awaken doubts as to whether any teratological change really arises "spontaneously," especially when we learn how slight a mechanical irritation of the growing point may induce changes in the flower; *e.g.* Sachs

showed that a sunflower head is profoundly altered by pricking the centre of the torus, and Molliard got double flowers by mechanical irritation.

Notes to Chapter XXVII.

For the details and classification of the multitude of facts, the student is referred to Masters' *Vegetable Teratology*. Ray Society, 1869, and the pages of the *Gardeners' Chronicle* since that date.

Concerning torsions, etc., the student should read De Vries, "On Biastrepsis in its Relation to Cultivation," *Ann. of Bot.*, Vol. XIII., 1899, p. 395, and "Hybridising of Monstrosities," *Hybrid Conference Report*, *Roy. Hort. Soc.*, 1900, Vol. XXIV., p. 69.

The reader will find an excellent account of the abnormalities in flowers due to the action of parasitic insects and fungi in Molliard, "Cécidies Florales," *Ann. des Sc. Nat.*, Ser. VIII., Bot., T. 1, 1895, p. 67.

CHAPTER XXVIII.

PROLIFERATIONS.

Proliferations—Vivipary—Prolepsis—Lammas shoots—Dormant buds—Epicormic shoots—Adventitious buds—Apospory and apogamy.

Proliferation consists in the unexpected and abnormal on-growing or budding out of parts—stems, tubers, flowers, fruits, etc.—which in the ordinary course of events would have ceased to grow further or to bear buds or leaf-tufts directly. Thus we do not expect a Strawberry—the swollen floral axis—to bear a tuft of leaves terminally above the achenes, but it occasionally does so, and similarly Pears may be found with a terminal tuft of leaves, Roses with the centre growing out as a shoot, Plantains (*Plantago*) with panicles in place of simple spikes, and so on.

We regard such cases as *teratological*, because they are exceptional for the particular species, and as *pathological* because they appear to be connected with over-feeding in soils with excessive

supplies of available food-materials ; but it should be noted that conditions quite comparable to proliferation are normal in the inflorescences of Pine-apples, some Myrtaceae, Conifers, etc., and that many instances of proliferations come under the head of injurious actions of fungi, insects, and other agents.

Proliferation of tubers is sometimes seen in Potatoes still attached to the parent plant in wet weather following a drought. The eyes grow out into thin stolons, or forthwith into new tubers sessile on the old tuber. Similarly in store we sometimes find the eyes transformed directly into new tubers, and cases occur where the growth of the eye is directed backwards into the softening tuber, and a small potato is formed inside the parent one.

Threading is also occasionally met with in the "sets" when ripened too rapidly in hot dry soils.

Vivipary is a particular case of proliferation, in a certain sense, where the seeds appear to germinate *in situ*, and we have small plants springing from the flowers, reminding us of wheat which has sprouted in the shocks in damp weather. In reality, however, the grains are here replaced by bulbils which sprout before they separate from the inflorescence. In varieties of *Poa*, *Polygonum*, *Allium*, *Gagea*, etc., this phenomenon is constant in plants growing in damp situations.

Proplesis.—It frequently happens that branches or whole plants are suddenly defoliated in summer,

—*e.g.* by caterpillars or other insects—at a time when considerable stores of reserves had already been accumulated during the period of active assimilation. In such cases the axillary buds, which would normally have passed into a dormant condition over the winter had the leaves lived till the autumn-fall, suddenly shoot out into *proleptic* shoots (also termed Lammas shoots), and re-clothe the tree with foliage. The wood of the year in which this occurs may exhibit a double annual ring, and the vigour of the tree is likely to suffer in the following season and no fruit be matured.

Proleptic branches may also be due to the shooting out of accessory buds—*i.e.* extra buds found in or near the leaf-axils of many plants, such as Willow, Maples, *Cercis*, *Robinia*, *Syringa*, *Aristolochia*, etc.—which do not normally come to anything, or do so only if a surplus of food materials is provided.

Dormant buds, or *preventitious buds*, are such as receive no sufficient supply of water and food materials to enable them to open with the other buds in ordinary years, for in most trees only the upper buds on the branches develop into new shoots. The lower buds do not die, however, but merely keep pace with the growth in thickness of the parent branch, and may be elongated sufficiently each year to raise the minute tips level with the bark, their proper cambium only remaining alive but not thickening the bud.

When, by the breaking of the branch above the insertion of the dormant bud—or by pruning, defoliation by insects, etc.—the transpiration current and supplies of food materials are in any way deflected to the minute cambium and growing points of the dormant buds, they are stimulated to normal growth, and may grow out as *epicormic shoots* or "shoots from the old wood." In many cases such epicormic shoots are stimulated to grow out by suddenly exposing an old tree to more favourable conditions of root-action and assimilatory activity, owing to the felling of competing trees which previously hemmed it in from light and air, and restricted the spread and action of its roots in the soil. This is often seen in old Elms, Limes, etc.

It is by such means as the above that substitution branches are obtained when a leader is broken or cut away.

Adventitious buds are such as are newly formed from callus or other tissues in places not normally provided with buds, as is often seen on occluding wounds—*e.g.* stool shoots. They may also be developed on roots, a fact utilised in propagating *Bouvardias*, Horse-radish, etc., by means of root-cuttings, and the *suckers* of Plums and other fruit trees are shoots springing from adventitious buds on roots.

Adventitious buds are also common on leaves (*e.g. Bryophyllum*, Ferns, etc.), and are frequently induced on them by wounds — *e.g. Gesneria*, *Gloxinia*, etc. Even cut cotyledons may develop

them, and pieces of leafless inflorescence (Hyacinth), hypocotyl (*Anagallis*), and in fact practically any wounded tissue with a store of reserve materials may be made to develop them: thus they have been found arising from the pith of Sea-kale, and are commonly developed from the cut bulb scales of Hyacinths.

Apospory and *Apogamy* are particular cases of the production of vegetative buds on the leaves in place of sporangia in Ferns (Apospory), and on prothallia in place of Archegonia (Apogamy), in the latter case induced by dry conditions and strong illumination.

Notes to Chapter XXVIII.

In addition to the literature quoted in the notes to Chapter XXVII., the student should consult the works on Forest Botany for the scattered information regarding adventitious buds. A good account may be found in Büsgen, *Bau und Leben unserer Waldbäume*, Jena, 1897.

For Apospory and Apogamy, see Lang "On Apogamy and the Development of Sporangia upon Fern Prothalli," *Phil. Trans.*, vol. 190, 1898, p. 187, where the literature is collected.

CHAPTER XXIX.

GRAFTS.

Grafting—Comparison with cuttings—Effects of environment—Relations between scion and stock—Variation in grafts—Grafting and parasitism—Infection—Pollination — Grafts-hybrids — Predisposition of Natural grafts—Root-fusions.

GRAFTING is a process which consists in bringing the cambium of a shoot of one plant into direct union with that of another, and is practised in various ways, the commonest of which is as follows :

One plant—the *stock*—rooted in the ground, is cut off a short distance above the surface of the soil, and a shoot from the second plant—the *scion*—cut off obliquely with a sharp knife, is inserted into a cleft in the stock, so that the two cambiums (and sometimes the cortex and pith of each as well) are in close contact : the scion is then tied in position, the wounds covered with grafting wax, and the whole left until union of the tissues is completed. This union depends on the for-

mation of *callus* at the cut surfaces, and the intimate union of the ingrowing cells from each callus.

The development of the callus follows the course described for wounds, cuttings, etc., and the union is exactly comparable to the union of the two lips of a healing callus over a wound (see p. 197).

Grafting was known and practised far back in the ages. Virgil was well acquainted with the process, and Theophrastus compared it with propagation by cuttings.

The scion differs from a cutting, however, in having no roots of its own : it is parasitic upon, or rather is in symbiosis with the stock, the root and tissues of which intervene between it and the soil. Consequently the selective absorption, size and number of vessels, and innumerable other physiological and anatomical peculiarities of the stock determine what and how much shall go up into the scion, while the latter supplies the former with organic materials and rules what and how much food, enzymes, and other secretions, etc., it shall receive to build up its substance. Surely, then, if such factors as the nature of the soil, the water and mineral supplies, the illumination, and the various climatic factors of altitude can cause variations on a plant direct, these and other factors are still more likely to be effective on stock and scion, and each must affect the other.

Nevertheless opinions have differed much as to whether any important effect is to be seen, and on

no point more than on whether the scion can affect the stock, in spite of such examples as *Cytisus Adami*, *Garreya* on *Aucuba*, Sunflower on Jerusalem Artichoke, etc. Recent results, especially of experiments with herbaceous plants, show that not only can the stock affect the scion (and *vice versa*) directly, but the effect of the changes may be invisible on the grafted plant and only show itself in the progeny raised from the seed of the grafted plant. In other words, variation occurs in grafts either *directly*, as the results of the effects of the environment on the graft, or owing to the interaction of scion and stock, showing as changes in general nutrition in the tissues concerned, etc., owing to special reactions of the protoplasm of the uniting cells one on the other, and of the results of the further protoplasmic secretions, sortings, and so forth, on the cells developed as descendants of these in the further growth of the graft: or *indirectly*, in that some of these changes so alter the nature of the special protoplasm put aside for reproductive purposes, that the resulting embryo in the seed transmits the effects, and they show as variations in the seedling. If these results are confirmed they should meet all objections that have been urged against the transmission of acquired characters.

In fact there are analogies between grafting and parasitism which cannot be overlooked, and should not be underestimated, their commonest expression appearing in the alterations in stature, habit, period of ripening, and so forth. These analogies

are easily apprehended when we compare parasites like the Mistletoe, *Loranthus*, or even such root-parasites as the Broom-rapes and the Rhinanthoideae with grafts; but they also exist in the case of many fungus-parasites, and we might almost as accurately speak of *grafting* some fungi on their hosts as of *infecting* the latter with them, especially when it is borne in mind that the effect of the scion on the stock is by no means always to the benefit of the latter, and that there are reasons for regarding the action of some such unions as that of a sort of slow poisoning of the stock by the scion. Why do we not here say that the stock has been *infected* by the scion?

The resemblances between pollination and the infection by fungus hyphae may also be insisted upon. If we take into account Darwin's remarkable experiments showing that in "illegitimate unions" the pollen exerts a sort of poisonous action on the stigmas or ovules, it is possible to arrange a series of cases starting with perfectly legitimate pollinations where the pollen tube feeds as it descends the style on materials provided by the cells, and proceeding to cases where the pollen is more and more merely just able to penetrate the ovary and reach the ovules, to the extreme cases where no union at all is possible.

Side by side with such series could be arranged analogous cases where fungus spores can enter and infect the cells of the host, and live symbiotically with or even in them, or can penetrate only with

difficulty, or with poisonous effects, and finally cannot infect the plant at all.

Less obviously, but nevertheless existing, are gradations in grafting to be observed, where one and the same stock may be successfully combined with a scion which improves it—or which is improved by it—or the scion may unite but acts injuriously on it, or, finally, cannot be induced to unite.

But we may go further than this in these comparisons. Just as the results of pollination frequently induce far-reaching effects on distant tissues—*e.g.* the swelling of Orchid ovaries, and rapid fading of the floral organs—so also the effects of hyphae in the tissues may induce hypertrophies, deflection of nutrient materials, and the atrophy of distant parts—*e.g.* the curious phenomena observed in *Euphorbia* attacked by *Uromyces*—and some of the distant actions in grafts may be compared similarly.

Going still further, we may compare the effects of cross-breeding or of hybridisation, where the *progeny* show that changes have resulted from the mutual interactions and reactions of the commingled protoplasm, with Daniel's results, in which he obtains proof of such interactions of the commingled protoplasmic cell-contents of grafts in the seedling progeny: although there is no probability—we may even say possibility—in this latter case that the effects are due to nuclear fusions, but only that the germ-plasm of the seed-bearing plant has been

affected by the changes in the cell-protoplasm which nourishes it when the reproductive cells are forming.

In the case of graft-hybrids the matter appears to be somewhat different, and we may well suppose, with Strasburger, that the commingling of characters observed in flowers, fruits, foliage, etc., on shoots borne after grafting are due to the occurrence of nuclear fusions during the union of the grafted tissues; though it is by no means impossible that what has really happened is profound alterations in the nuclear substance (germ-plasm) owing to its being nourished by cell-protoplasm (somato-plasm) which has been itself affected by the interchanges of substance between scion and stock, and therefore itself furnishes a different nutrient medium from the unaltered cytoplasm of either.

But even here we can find parallels among the ordinary phenomena of plant reproduction. Maize plants with white endosperm containing starch, if crossed by pollen from other plants with purple endosperm containing sugar, bear seeds with purple endosperm containing sugar, and such *Xenia* may be compared to graft-hybrids in many respects.

I know of no case among fungus infections which could be compared directly with these examples, and it is not at all likely that we shall meet with any instance of a fungus-hypha handing over nuclear substance to an egg-cell, and so affecting the latter that an embryo results.

But the case is not hypothetically impossible, although the distant relationships of the two groups of organisms render it extremely improbable among the higher plants. It is by no means so improbable, however, that further research may show cases where the egg-cell of a lower cryptogam—*e.g.* another fungus—may be affected either directly, or indirectly, by the protoplasm of a parasitic or symbiotic hypha, as suggested by the extraordinary phenomena of symbiosis.

Some of the variations in grafted plants are found to predispose the plant to disease, or the reverse, and cases may be cited where the resulting shoots, foliage, or fruits, or seedlings more readily fall a prey to, or resist, parasitic fungi and insects than the ungrafted plants. Daniel gives instances of such—*e.g.* among other examples, Peas grafted on Beans yield seeds which suffer more from Erysipheae than the normal seedlings. But the best known cases are those of Vines in their relations to *Phylloxera*, already referred to (p. 155).

Several instances are also known where grafted plants show more or less resistance to such factors of the environment as low temperatures; grafted or budded Roses often suffer much from Erysipheae, and so forth. Much research is still needed to determine how far these matters depend on real alterations in the nature of the graft, or *are only true for the localities in which the experiments have been made*, a point which has, I think, been overlooked by all observers.

Grafted plants are apparently very much exposed to injury by slugs, insects, and the invasions of parasites during the healing of the callus and the fusion process. Here again it must not be overlooked that the callus is, so to speak, a tit-bit of luscious, thin-walled, succulent tissue ; and, like all wounds, the graft affords entrance to parasites such as *Nectria* and Ascomycetes of various kinds, under circumstances very favourable to their invasion.

Natural Grafts.—It is by no means an uncommon event to find the branches of Beeches, Limes, and other trees which have been accidentally brought into contact during growth, joined where they cross. As they press one against the other, they become naturally grafted, by that form of the process known as *inarching* : except that in artificial inarching the operator cuts off the cortical tissues of the two branches and brings their cambial surfaces together, whereas in nature the cambiums only come into contact after the destruction by pressure, or slight abrasion, of the entrapped intervening tissues. The fusion occurs, in fact, exactly as in the burying-in of a nail or wire, referred to on p. 211.

Natural grafts are very common among the roots of trees, and possibly explain some queer cases of the apparent revivification of stumps of trees not usually given to forming abundant stool shoots. It is regarded as probable in some old forests that the majority of the roots of trees of the same species are linked up together by such

natural grafts, a probability not diminished by the fact that such roots cross at many points, and are easily grafted.

Notes to Chapter XXIX.

The student should read Bailey, *The Nursery Book*, 1896, for details regarding the practice of grafting, and facts in abundance can be obtained from the pages of the *Gardeners' Chronicle.*

Concerning graft-hybrids and the variations of grafted plants see Jouin, *Can Hybrids be obtained by Grafting?* and especially Daniel, "La Variation dans la Greffe," in *Ann. des Sc. Naturelles*, S. VIII., Vol. 8, 1898, p. 1, and the literature there collected. The whole subject is largely controversial, and much work remains to be done.

CHAPTER XXX.

LIFE AND DEATH.

Protoplasm — Hypothesis as to its structure and behaviour — Assimilation — Growth — Respiration — Metabolism—Action of the environment—Nuclear protoplasm — Pollination — Grafting — Parasitism — Graft-hybrids — Life — Death — Variation — Disease.

We have seen that all the essential phenomena of disease concern only the living substance—the protoplasm—of the plant, and that however complex the symptoms of disease may be, the occurrence of discolorations, lesions, hypertrophies, and so forth are all secondary matters subsidiary to the fundamental alterations of structure and function constituting the disease. It remains to see if we can adopt any hypothesis as to the nature of this physical basis of life—the protoplasm—which shall help us to understand still more clearly in what must reside those processes which, so long as they proceed harmoniously and uninterruptedly, constitute life and

health, and which when interfered with result in disease and death. The protoplasm of the living plant-cell looks like a slimy translucent mass which has been superficially compared in appearance to well-boiled sago or clear gum. Fifty years of observations and experiments with it have convinced physiologists that it is not a mere solution or emulsion, however, or even a chemical compound in the ordinary sense of the term, although chemical analysis gets little out of it beyond water, proteids, carbohydrates and fats, and traces of certain mineral salts; for living protoplasm does not respond to the laws of physics and mechanics in obeying them, simply as do ordinary solutions and liquids. On the other hand, the most delicate chemical manipulation fails us, because when killed it is no longer protoplasm. Nor does the microscope advance matters far, beyond convincing us that this marvellous material must have a structure far more intimate than anything visible to the highest magnifying powers at our disposal.

Nevertheless, some information is forthcoming from the comparative examination of the protoplasm of numerous different kinds of organisms, for we have learnt that certain ingredients and no others are necessary for its composition—namely, carbon, hydrogen, oxygen, nitrogen, phosphorus, sulphur, calcium,[1] magnesium, potassium—and it is as a rule of no use trying to foist on to it any substitute for any one of these. Moreover, these

[1] See note at end of chapter.

chemical elements must be given in certain definite proportions and forms: for instance it is of no use to offer the carbon and sulphur in such a form as carbon disulphide, or the nitrogen and hydrogen in that of hydrocyanic acid, but the carbon must be given to the protoplasm in the form of a carbohydrate or in some similar form, the nitrogen as an ammonium salt, nitrate or proteid, the sulphur as a sulphate, and so forth, and thus water, air, carbohydrates, and the nitrates, sulphates, and phosphates of potassium, calcium, and magnesium become the chief natural sources of the essential ingredients. Again, we have learnt that while there are different forms of protoplasm in the cell, and that these react on each other, and go through cycles of arrangement and rearrangements, the intimate structure must be of that kind termed molecular—beyond the region of vision, just as is the microscopic structure of a crystal; but, while like the latter affording evidence of order and sequence when properly examined, the structural arrangements and changes must be infinitely more complex.

All these, and numerous other results of enquiry, have led to the conclusions that we must regard living protoplasm as a complex made up of very large molecular units, each containing atom-groupings of the elements named; and, partly on account of the large number of atoms they contain, and partly due to the vibrations of absorbed heat, these units must be extremely labile. Moreover, they are linked up into an

invisible and intricate meshwork, bathed in a watery liquid held in the interstices somewhat as water is held in a sponge. In this imbibed liquid are dissolved the substances, consisting of the same elements, which are to serve as food, and which are to be taken up into the molecular framework and built up into the structure of new molecular units—or, as they may be shortly termed, molecules of protoplasm: in the bathing liquid are also dispersed the fragments—again containing the elements named—which have resulted from the breaking asunder of some of the complex protoplasm molecules, and which are partly destined to be used up again, partly to be burnt off in respiration, and partly to be put aside as metabolic products such as reserves, secretions, permanent structure, etc. Among the elements carried into this liquid and dissolved in it the free oxygen of the air also plays an important part.

As new molecules are formed, by mutual combinations of the food-materials selected by molecular attractions, they are taken up into the protoplasmic framework, and built in between those already in existence, thus distending the whole, and we say that the protoplasm *Assimilates* food-materials and *Grows*. When distended beyond a given degree, or disturbed in various other ways, the molecular framework breaks, and some of the molecules are shattered, and as they fall to pieces certain of their constituent parts containing carbon and hydrogen forcibly combine at the moment of liberation with the oxygen in

the fluid around and are burnt off in the form of carbon-dioxide and water, heat being of course evolved. This is the fundamental process of *Respiration.*

It is probably the alternation of these processes of *Assimilation*—the building up into the protoplasmic structure of new complex labile molecules—and *Destruction*—the shattering of such molecules with redistribution, oxidation, etc., of their fragments—which constitute the fundamental process of life. Different authorities attempt to explain the details of these processes in various ways, but there is practical agreement on the one point, that life consists in the alternate building up of new protoplasm from the food-materials—*Assimilation*—and the breaking down of the molecular complexes to simpler ones —*Disintegration*, or *Dis-assimilation*, as we may call it. During the periods when assimilation prevails, and the protoplasm increases in mass, we recognise *Growth*, and since this is usually associated with the vigorous imbibition of water, owing to the powerful osmotic attractions for that liquid exhibited by some of the products, and with consequent further stretching of the invisible molecular plexus, the growth may be so evident in increased size, that we are accustomed to look upon the visible increase in volume alone as growth; but it is essential to understand that growth of the protoplasm is always proceeding during life, even when as many older molecules are being shattered and dispersed as new ones

are being formed by assimilation, and when, therefore, no visible permanent enlargement occurs. Similarly, during periods when disintegration of the molecules prevails, we must not assume that the assimilation of new molecules is not occurring and that growth is not proceeding. The two processes are always going on during the active life of the protoplasm: in fact life consists in the play of these processes, as already said.

That numerous chemical rearrangements of the atom-complexes take place outside the protoplasmic molecules—both of those left unemployed in assimilation and of those rejected during the destructive processes—will be readily understood: many of the bye-products found in plants, such as vegetable acids, alkaloids, colouring matters, crystalline bodies, etc., etc., are due to these, so to speak, fortuitous combinations and re-combinations.

The part played by respiration has often been misunderstood. It consists in the burning off of some of the carbon and hydrogen of the shattered protoplasm molecules, by means of the oxygen of the air, which finds its way into the fluids around the protoplasm, and when it is active every act of combustion—which is here an explosion—leads to the shattering of more protoplasm molecules, and consequently to more respiratory combustion of the products. If the supply of oxygen is limited the breaking down of the molecules of protoplasm does not cease, but the carbon and hydrogen which would otherwise have been

oxidised are now in part left to form other compounds in the surrounding liquid, and thus incompletely oxidised bodies, such as vegetable acids, alcohols, etc., accumulate. Even in the complete absence of atmospheric oxygen the protoplasm may go on breaking down and accumulating various compounds containing relatively much carbon and hydrogen—so-called intramolecular respiration ; but in ordinary plants this process soon comes to an end, because the blocking up of the molecular plexus leads to obstruction and interferes with the normal assimilation and dis-assimilation, and, if prolonged, leads to pathological conditions, and eventually death.

Here, then, we meet with a cause of disease, or of predisposition to disease. The deprivation of oxygen interferes with the normal processes of building up and breaking down of the protoplasmic molecules, and bodies we term poisonous accumulate and may lower the vitality or even bring life to an end.

During normal life other products of the disruption of the protoplasm molecules are nitrogenous bodies, such as proteids, and these we have reason to believe are used up again, acting as the nuclei, so to speak, of the new molecules, and so being built up again with fresh food-materials into the plexus, to be again set free, and again used up, and so on. Others are the carbohydrates, such as cellulose, which pass out of the molecule into an insoluble form, and are accumulated outside the protoplasm in the form of cellulose membranes, and so forth.

It is these formed products of metabolism (Metabolites), especially cellulose and bodies which result from its subsequent transformation, which constitute the main permanent mass of the ordinary plant.

We are now in a position to see how another fundamental cause of disease or predisposition to disease exists in the deprivation of the protoplasm of any of the elements needed to supply—in the food-materials—the place of those which have been permanently put aside in the form of cell-walls, or burnt off in respiration, passed out as excretions, or in other ways lost.

It is clear that the indispensability of an element must mean that the protoplasmic molecule cannot be completed without it: the same conclusion is supported by the experimental proof that these elements cannot be replaced by chemically similar elements.

It does not follow, however, that the protoplasm molecule must always have the same number of atoms of these elements, and grouped always in the same atom-complexes before being assimilated; nor that the protoplasm molecule, when once built up, always breaks down in exactly the same way. On the contrary, while the protoplasm of corresponding parts of a daisy and of a rose must contain all the elements named, we must believe that the atom groupings are different in the protoplasm molecule in each case; and though the molecules of the cell-protoplasm, of the nucleus, of the chlorophyll-corpuscles, etc., of one

and the same plant must have all these elements, the atom groupings and modes of building up and breaking down may be very different in each case.

Again, the cell-protoplasm, bathed by the sap taken in by roots from the soil or fed directly by that derived from the leaves, must be exposed to very different stimuli and modes of nourishment, etc., from those incurred by the protoplasm of the nucleus which it encloses: and similar conclusions must apply in turn to the protoplasm of the root in the dark moist soil and of the leaf in the light dry air, or to that of the superficial epidermis cells as contrasted with that of the deeply immersed pith, and so on.

It is no doubt in these directions that we must seek for the explanation of many life-phenomena at present quite beyond explanation. Thus, it is tolerably easy to modify the action of the cell-protoplasm of a plant, by exposing it to differences of illumination, temperature, moisture, and so forth, within certain limits; at least, since the changes in stature, tissue differentiation, cell-secretions, flowering capacity, etc., of plants affected by such factors of the environment—*e.g.* alpine plants brought into the plains—*must* be due to changes in the mode of activity of the protoplasm, we must assume that the above factors affect the latter. But it is extremely difficult to reach the nuclear-protoplasm directly by such stimuli, as proved by the experience that even where we allow the factors to act for a long time, no permanent change can be

detected in the behaviour of the nuclear-protoplasm—the essential material in the reproductive organs and reproductive process. At least we must infer that no change has been permanently stamped on this nucleo-plasm from such facts as the characters of the seedlings of the progeny of the plain-raised plants: if they are again sown in an alpine situation they forthwith behave again as alpines.

Must we not conclude, then, that this difficulty of reaching the nuclear-protoplasm is owing to the fact that it is nourished and influenced directly only by the cell-protoplasm? That the cell-protoplasm is its environment, and not so directly the outer world? We may influence the cell-protoplasm—we may make it work harder or less actively, respire vigorously or slowly, build up and break down in various different ways, or at different rates, and so forth, *within limits*; but it is nevertheless cell-protoplasm of its specific kind, with its own range of molecular variations and activities within these limits, and it supplies the nuclear-protoplasm with what it wants so long as these limits are not exceeded. Consequently, while it is very easy to make the cell-protoplasm vary within the limits of its range, it is not easy to induce it to vary its effects on the nuclear-protoplasm to such an extent or in such a way that the latter is permanently or materially altered in constitution.

Nevertheless it would appear that cases do occur where the nuclear-protoplasm *is* reached and

affected by external stimuli, as evinced by some of the phenomena of hybridisation and of cross- and self-fertilisation, because we find the results expressed in the mingling of the characters of parents, in strengthened or enfeebled progeny, and even in the appearance of unexpected properties, which, from the facts of Reproduction, we know must have taken their origin in some alteration of the nuclear substance of the embryo.

Here, however, we know in most cases that the principal agent which has reached the nuclear-protoplasm, is another portion of nuclear-protoplasm. In hybridisation, one which has been fed and influenced by cell-protoplasm of a very different plant; in cross-fertilisation, one fed and influenced by the cell-protoplasm of a different plant of the same species, and in self-fertilisation, one fed and influenced by the same cell-protoplasm.

That somewhere, and somehow, such nuclear-protoplasm as induces the changes in the characters of hybrids, etc., has been influenced by its immediate environment—the cell-protoplasm of the plant—appears to be a conclusion from which there is no escape. We may obtain similar evidence from the experience of grafting. It is relatively easy to influence the cell-protoplasm of a scion by a suitable stock, obviously because the latter, while handing on to the former all necessary materials from the soil, presents the indispensable elements and compounds in somewhat different proportions, dilutions, etc., from those which its

own roots would have done, and probably mingles with them a certain amount of its own peculiar products, as well as affects the modes of working and interaction of both by the molecular impetus impressed on them. Consequently the cell-protoplasm of the scion, while obtaining from the stock all it needs within the limits of its own variations of structure and activity, nevertheless builds up and breaks down in ways or at rates slightly different from those hitherto normal to it, and perceptible variations result when the sequences and correlations of these material and mechanical changes have affected a sufficiently large mass for the accumulation of visible effects. The limits to grafting suggest not that an inappropriate stock does not offer to the protoplasm of the scion the right materials, but that it presents them in proportions and in forms which are unsuitable for the assimilable powers of the latter, or, possibly, mingled with substances poisonous in themselves or capable of becoming so in conjunction with bodies in the scion.

What has been said of the action of stock on scion, will also be true, *mutatis mutandis*, of the reciprocal action of scion on stock. Here again we may have causes for disease, or predisposition to disease.

It occasionally happens, however, that the nuclear protoplasm of the stock or scion *is* affected in grafting, and we infer from the difficulty of modifying it in any other way in ordinary reproduction than by means of other nuclear protoplasm

—*e.g.* in hybridisation—that in such cases a fusion of the nuclei of stock and scion has occurred during the grafting, and a *graft-hybrid* has resulted—*e.g. Cytisus Adami.*

It is not impossible however that the nuclear protoplasm has in such graft-hybrids been subsequently modified by the differences in nutrition to which it has been subjected, in the modified cell-protoplasm affected by the mingling of the juices, etc., of scion and stock; for it is quite conceivable that such materials may affect the protoplasm far more profoundly than anything derived directly from the environment.

If Daniel's researches are confirmed, however, it appears that in some cases, at any rate, the nuclear-protoplasm is so altered by the grafting that when the new embryo is developed, after fusion with nuclear substance from another plant of the same species, the results are apparent only in the progeny, and *the effects of alteration in the cell-protoplasm have been transmitted to the nuclear protoplasm of the germ-cells—i.e.* acquired characters have been transmitted and fixed by heredity. Should this prove true the importance of the results can hardly be over-estimated. The matter is too problematical for further discussion here, but we see that any such action may profoundly affect the "constitution" of the resulting plant.

Turning now to the case of fungi or other organisms which obtain access to the cell-protoplasm. At the one extreme we have cases where the protoplasm of the diseased plant is rapidly and directly

poisoned and destroyed, as in the killing off of seedlings in "Damping Off": near the other extreme we have cases where the foreign protoplasm of the parasite, although it gains complete access to that of the host, merely stimulates the latter to greater activity and itself works for its own ends in conjunction with it—*e.g. Plasmodiophora*. In such instances we must figure to ourselves the cells of the root of the Crucifer handing on food-materials to both masses of protoplasm—that of the *Plasmodiophora* and that of the cell into which it penetrates; and it is immaterial whether both obtain the food-materials directly, or, what seems more likely, the fungus only at second hand and by the medium of the host's protoplasm. In any case, the latter is for a long time at least not poisoned or maimed, or in any perceptible way injured by excreta from the fungus-protoplasm, although it is evident that each must excrete various metabolites which may soak into and be taken up by the other: on the contrary the host-protoplasm grows larger, attracts more food supplies, makes larger cells, and is evidently stimulated to greater activity for the time being, its behaviour reminding us of the stimulation of cells by means of slight doses of poison referred to previously. We must therefore assume that the general course of building up and breaking down of its protoplasm-molecules go on as usual —or nearly so—in both the host cell and the invader; and that the assimilatory, respiratory, excretory and other functions are carried on in

the former as in the normal cell, or are but slightly modified to an extent which does no immediate injury to its life. But we must further assume that the same is also true of the invading protoplasm, and that the *Plasmodiophora* is also supplied with suitable atom-complexes to build up its protoplasm molecules, as fast as they are shattered and the rejecta burnt off in respiration.

A step further, and we come to instances of *Symbiosis*, where the commingled masses of protoplasm of host and invader continue this harmonious action during life. Clearly there are resemblances between these latter cases and successful grafts, and between both and successful sexual unions where the resulting embryo-cell gives rises to a vigorous and healthy plant; and the more these resemblances are examined in the light of what we know of symbiosis the more they support our contention.

Such considerations as the foregoing suggest, then, that life consists in the regular and progressive building up and breaking down of the complex protoplasm molecules, and is necessarily accompanied by the influx of the indispensable food-elements in certain combinations and atom-complexes for assimilation, and by the combustion of some of the débris of the shattered molecules, which combine with the oxygen in respiration and so afford explosions which raise the temperature and enhance the lability of existing molecules, and act as stimuli to the shattering of further molecules. The results of these rhythmical buildings

up (assimilation) and shatterings (dis-assimilation) of the protoplasm molecules are the growth of the protoplasm, with further intercalations of water and new food-supplies, etc., on the one hand, and the formation of metabolic products (proteids, cellulose, sugars, fats, etc.), some of which are again used up, others respired, others deposited as stores, cell-walls, etc., on the other.

That the building-up process depends on the action of molecular forces comparable to those by which a growing crystal goes on selecting atom-complexes of its particular kind from the solution around seems highly probable, and this being the case we can understand how under certain circumstances *substitutive* selections may occur. That is to say, just as a crystal will sometimes build up into its structure atom-complexes of a kind different from its normal molecules, so, given the proper conditions, a protoplasmic molecular unit will build up into its structure atom-complexes somewhat different from those it had hitherto taken up — *i.e.* assimilated — with consequent modifications of its behaviour. If this occurs, the modes of further building up and breaking down will be affected by the subsequent action of these slightly modified protoplasm units, *and it may well be that the whole significance of variation turns on this.* Whether the resulting variation makes for the welfare or otherwise of the organism will then be decided by the struggle for existence, and the natural selection which ensues. Such a view also implies that the

energy concerned is primarily what is usually termed chemical energy, and that every compound entering into the protoplasm carries in a supply of this, available in various ways.

Death, on the contrary, is the cessation of these rhythmical processes of building up and breaking down of the protoplasm molecules. It does not imply the cessation of chemical changes of other kinds, but that these rhythmical constructions of the complex and labile protoplasm molecules breaking down on stimulation to bodies partly re-assimilable, partly combustible in respiration, and partly excretory, etc., have ceased, and that further chemical changes in the material are thenceforth simpler and different in kind and degree, eventually leading to total disintegration so that no units are left capable of restoring the rhythm.

If these ideas are correct, we may define *Disease* as dangerous disturbances in the regularity, or interference with the completeness or range of the molecular activities constituting normal Life—*i.e.* Health—and it is evident that every degree of transition may be realised between the two extremes. Now, if we further assume, as I think we must do, that a considerable range or "play" must exist in the molecular activities of the protoplasm constituting life, we obtain a sort of expression of what we mean by limits of variation. The fact that life can go on in a given plant at temperatures between from 1°-5° and 35°-40° C., or in lights of different intensity, or within

considerable ranges of water supply, concentration of salts, partial pressure of oxygen, etc., implies that the molecular activities of the protoplasm are of the normal *kind* all the time, though they may differ in rapidity, and even in *quantitative* and *qualitative* respects within certain limits; and the meaning of the *optimum* temperature, illumination, oxygen pressure, etc., is, from this point of view, not that the molecular activities differ in kind from those nearer the minima and maxima, so much as that they are running at the best rates for the welfare of the plant—*i.e.* for permanent health.

If we transcend the cardinal points limiting the range of this play, however, and we get variations in the *kind* as well as *rates* of molecular constructions and disruptions, then we pass by imperceptible gradations into ill-health—*i.e. Disease.*

And similarly in relation to other protoplasm. That of the right kind of pollen grain from another plant of its own species, stimulates the contents of the ovule to produce a vigorous embryo and healthy seedling: that of a similar pollen grain in its own flower either does no positive harm, but has a feebler effect, or it may act like a poison. That of another pollen grain again may refuse to unite at all; while that of a fungus hypha—*e.g.* of *Sclerotinia* on *Vaccinium*—may run down the style as does the pollen tube and produce death and destruction throughout the ovule.

Or again, in Clover, we may have the hypha of a *Botrytis* with its protoplasm unable to do more

than penetrate into the cellulose walls and diffuse a poison into the adjacent cells, being utterly incapable of directly facing, or mingling with the living protoplasm of such cells, whereas the protoplasm of another organism—*e.g. Rhizobium*—will penetrate directly into the cells, live in them for weeks or months without injury—nay even with advantage to their life. And hundreds of similar cases can be selected.

We may, therefore, conclude that *Variation* depends fundamentally on alterations in the structure or mode of building up and disintegration of the protoplasmic molecular unit, brought about either by direct modifying action of the inorganic environment—nutrition, temperature, oxygen supply, light, etc., etc.—or by the mingling with it of other protoplasm, the molecules of which since they have already a slightly different composition, configuration, mode of breaking down and building up, etc., affect its molecules by supplying them with altered nutritive atom-complexes, by competing with them for oxygen, etc., etc. Once these molecules are affected, we must assume that long sequences of other chemical and molecular changes will be also modified; and although we have no conception of *how* these changes bring about changes in form, that they do so is only a conclusion of the same order as that which we hold regarding the much simpler changes concerned in the formation of crystals.

That such variations may be of every degree as

regards profundity, permanence, kind, etc., may well be imagined; and there is nothing surprising in our being able to induce them more easily by the action of external factors *in the readily accessible cell-protoplasm* than in the *less exposed nuclear-protoplasm;* because the latter is only accessible through the former, or through the agency of *other nuclear protoplasm already modified.* On these and similar phenomena depend the relative permanency and transmissibility of the variations. Our measure of the latter only begins when the effects referred to have become manifest in large masses of cells, because only then do they become appreciable to our senses.

Further, variations thus induced may be of advantage to the continued life of the plant, or in all degrees disadvantageous or threatening to its existence. These latter variations are *Disease*, and if their interference with the normal rhythmical play of the building up and breaking down of the protoplasm molecules proceeds beyond certain limits, life ceases, and we have death supervening on disease.

Notes to Chapter XXX.

It appears probable that calcium is not always needed by living cells, and may not enter into the composition of protoplasm; on the other hand traces of iron are perhaps necessary.

The criticisms and summary of facts on which the hypothesis regarding protoplasm here adopted is based are developed at length in Kassowitz, *Allgemeine Biologie*,

Wien, 1899, B. I. and II., where the collected literature may be found, and the reader introduced to the huge mass of controversial writings put forward since Darwin and associated with the names of Weismann and others.

It will probably be noticed that I have employed the term molecular unit of protoplasm, and have not discussed the question of organised structure in the latter: this is because it seems clear to me that living protoplasm as such does not possess "organised structure" in the true sense of that term—it is, rather, busy preparing and making "organised structure," and a molecular constitution would have to be ascribed to all "physiological units" of the nature of micellæ, pangens, ids, etc., as truly as to the structural units of a starch-grain or cell-wall, or even of a crystal. In this connection, the student will find the necessary points of view put forward in Pfeffer, *Physiology*, pp. 37-83.

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